

## Modeling the biodiversity crisis : the roles of space and strategic behavior in bioeconomic modeling

*Modéliser la crise de la biodiversité : les rôles de l'espace et  
des comportement stratégiques dans la modélisation  
bioéconomique*

### **Thèse de doctorat de l'Université Paris-Saclay**

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**Titre:** Modéliser la crise du vivant : les rôles de l'espace et des comportements stratégiques dans la modélisation bioéconomique

**Mots clés:** Modélisation bioéconomique; Biodiversité; Connectivité Spatiale; Exploitation et Contrôle; Equilibre non coopératif; Politique Publique

**Résumé:**

La biodiversité mondiale subit des pressions croissantes dues aux activités humaines : perte d'habitats, surexploitation des ressources, changements climatiques, introduction d'espèces invasives. Ces menaces affectent non seulement la diversité des espèces, mais aussi les services écosystémiques essentiels. Les politiques de conservation, malgré les initiatives internationales et nationales, ont des performances mitigées.

Comment mieux concevoir des politiques pour freiner l'effondrement de la biodiversité tout en prenant en compte les enjeux économiques ? Comment intégrer l'espace à l'analyse économique de la biodiversité ? Comment intégrer les interactions entre agents stratégiques autour de la biodiversité ?

Cette thèse modélise la perte et fragmentation de l'habitat ainsi que la surexploitation (ou le sous contrôle) des espèces en utilisant une approche bioéconomique, qui combine l'économie d'une part et l'écologie des populations et des paysages d'autre part. Elle met l'accent sur le rôle de l'espace et les interactions stratégiques, afin d'orienter les politiques publiques dans divers écosystèmes.

Le premier chapitre passe en revue la littérature bioéconomique sur les systèmes socio-écologiques terrestres, et identifie deux grands paradigmes : l'optimisation économique des ressources et la conservation de la biodiversité dans des paysages aménagés. Il expose les défis méthodologiques de la modélisation bioéconomique pour mieux saisir la crise de la biodiversité, et apporter des pistes de solutions.

Le deuxième chapitre développe un modèle de gestion des paysages forestiers confrontés au dilemme entre conservation et réduc-

tion des risques d'incendie. En utilisant la théorie des graphes, il définit une frontière de production entre ces objectifs sous contrainte budgétaire et caractérise les localisation des opérations de traitement des combustibles optimales, ainsi que les paysages qui en découlent.

Le troisième chapitre traite de la gestion des espèces nuisibles en intégrant l'usage de clôtures écologiques. Le modèle explore comment ces barrières limitent la propagation d'espèces nuisibles dans un réseau de parcelles, en intégrant des coûts de contrôle hétérogènes. Il considère la question des externalités spatiales, et de la gestion des opportunités d'arbitrage spatiales. Il propose une analyse de la connectivité des paysages comme décision et examine la gestion optimale et non coopérative des espèces nuisibles mobiles.

Le quatrième chapitre analyse l'exploitation du Totoaba macdonaldi, un poisson en danger critique à cause du braconnage d'un cartel. Il revisite un modèle bioéconomique et analyse les conséquences d'un monopole vertical sur le totoaba. Il montre ensuite que l'aquaculture peut réduire la pression sur les populations sauvages, contrairement à l'idée que celle-ci intensifie l'exploitation. L'élevage de totoaba stabilise les populations et réduit les incitations au braconnage, avec des implications importantes pour la conservation.

En conclusion, cette thèse propose des développements dans la modélisation bioéconomique, en prenant en compte l'espace et les comportements stratégiques, pour analyser la crise de la biodiversité, ouvrant la voie à des politiques publiques plus efficaces conciliant conservation et développement économique.

**Title:** Modeling the biodiversity crisis : the roles of space and strategic behavior in bioeconomic modeling

**Keywords:** Bioeconomic modeling; Biodiversity; Spatial Connectivity; Harvest and control; Non cooperative equilibrium; Public policy

**Abstract:**

The world's biodiversity is under increasing pressure from human activities: habitat loss, overexploitation of resources, climate change, and introduction of invasive species. These threats affect not only species diversity but also essential ecosystem services. Despite international and national initiatives, conservation policies have had mixed results.

How can we better design policies to halt the collapse of biodiversity while taking economic issues into account? How can we integrate space in the economic analysis of biodiversity ? How can we integrate the interactions between strategic agents around biodiversity?

This thesis models habitat loss and fragmentation, as well as the overexploitation (or undercontrol) of species, using a bioeconomic approach that combines economics on the one hand, and population and landscape ecology on the other. It focuses on the role of space and strategic interactions in order to guide public policies in various ecosystems.

The first chapter reviews the bioeconomic literature on terrestrial social-ecological systems and identifies two major paradigms: economic optimization of resources and biodiversity conservation in managed landscapes. It outlines the methodological challenges of bioeconomic modeling to better grasp the biodiversity crisis and provide possible solutions.

The second chapter develops a management model for forest landscapes faced

with a dilemma between conservation and wildfire risk reduction. Using graph theory, it defines a production frontier between these objectives under budgetary constraints, and characterizes the locations of optimal fuel treatment operations, as well as the resulting landscapes.

The third chapter deals with the management of pest species by integrating the use of ecological fences. The model explores how these barriers limit the spread of pest species in a network of plots, integrating heterogeneous control costs. It considers the issue of spatial externalities and the management of spatial arbitrage opportunities. It proposes an analysis of landscape connectivity as a decision and examines optimal and non-cooperative management of spatial public bads.

The fourth chapter analyzes the exploitation of *Totoaba macdonaldi*, a critically endangered fish due to cartel poaching. It revisits a bioeconomic model and analyzes the consequences of a vertical monopoly on totoaba. We then show that aquaculture can reduce pressure on wild populations, contrary to the idea that it intensifies exploitation. Totoaba farming stabilizes populations and reduces incentives for poaching, with important implications for conservation.

In conclusion, this thesis proposes developments in bioeconomic modeling, taking into account space and strategic behaviors, to analyze the biodiversity crisis, paving the way for more effective public policies reconciling conservation and economic development.

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# Introduction en français

L'humanité se trouve dans une ère écologique critique, où les seuils écologiques du système terrestre ont été franchis. La notion de "frontières planétaires" (Rockström et al., 2009; Steffen et al., 2015) illustre la façon dont l'anthroposphère, les effets des activités humaines à l'échelle de la planète, est devenue une composante fonctionnelle supplémentaire et est capable de modifier le système terrestre (Richardson et al., 2023) aux côtés de la géosphère (flux d'énergie et matériaux non vivants de la Terre et de l'atmosphère) et de la biosphère (tous les organismes vivants/écosystèmes). Le cadre des "limites planétaires" identifie les limites de l'impact de l'anthroposphère sur le système terrestre qui peuvent sauvegarder l'état interglaciaire de la Terre - le seul où la civilisation est connue - en identifiant un "espace opérationnel sûr". Parmi ces neuf limites, Richardson et al. (2023) estime que six ont été franchies, menaçant la stabilité et la résilience du système terrestre.

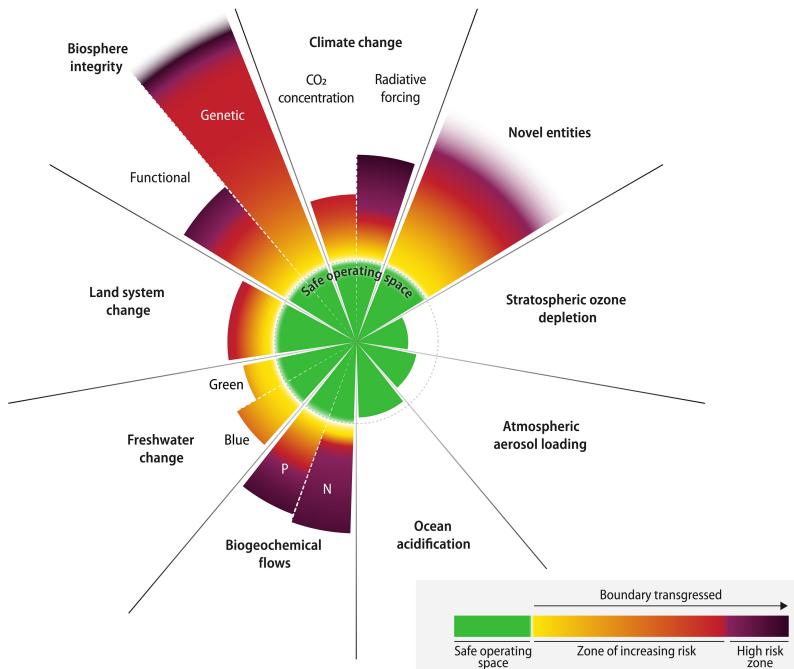


Figure 1: État actuel des variables de contrôle pour les neuf limites planétaires, à partir de Richardson et al. (2023)

Parmi ces limites planétaires, l'intégrité de la biosphère a progressivement suscité un intérêt particulier, de même que son interaction avec d'autres lim-

ites, telles que le changement climatique, ou des entités nouvelles (par exemple, les polluants organiques synthétiques, les matières radioactives, la pollution microplastique...). Créé en 2012, le Groupe Interdisciplinaire sur la Biodiversité et les Services Ecosystémiques (IPBES<sup>1</sup>) a tiré la sonnette d'alarme sur l'état de la « nature » à l'échelle mondiale. Son président, Sir Robert Watson, l'a clairement exprimé<sup>2</sup> :

*Les preuves accablantes du Rapport d'Evaluation Global de l'IPBES (2019), provenant d'un large éventail de domaines de connaissances, présentent un tableau inquiétant [...]. La santé des écosystèmes dont nous et d'autres espèces dépendons se détériore plus rapidement que jamais. Nous sommes en train d'éroder les fondements de nos économies, de nos moyens de subsistance, de notre sécurité alimentaire, de notre santé et de notre qualité de vie dans le monde entier<sup>3</sup>*

La « nature » est un concept central dans le cadre de l'IPBES (IPBES, 2019) :

*La nature (également définie comme la nature vivante) [est] le monde non humain, y compris les caractéristiques coproduites, avec un accent particulier sur les organismes vivants, leur diversité, leurs interactions entre eux et avec leur environnement abiotique. Dans le cadre des sciences naturelles, la nature comprend, par exemple, toutes les dimensions de la biodiversité, les espèces, les génotypes, les populations, les écosystèmes, la biosphère, le fonctionnement des écosystèmes, les communautés, les biomes, les systèmes de maintien de la vie sur Terre et leurs processus écologiques, évolutifs et biogéochimiques associés, ainsi que la diversité bioculturelle. Dans le cadre de l'économie, il comprend des catégories telles que les ressources naturelles biotiques, le capital naturel et les actifs naturels. Dans le contexte plus large des sciences sociales et humaines et des sciences environnementales interdisciplinaires, il est fait référence à des catégories telles que le patrimoine naturel, l'environnement vivant ou le non-humain. Dans le contexte d'autres systèmes de connaissance, il comprend des catégories telles que "Terre mère" [...], "Pachamama" [...]. IPBES (2019), p.14, voir aussi Diaz et al. (2015)*

La nature, telle qu'elle est définie dans cette approche, est un objet très vaste et complexe. Elle se définit à travers des différences ontologiques et épistémiques (vivant et non-vivant), différents types d'interactions, à diverses échelles (génotypes v. écosystèmes), à différents types de processus (biologiques v. écologiques), et à travers différents champs d'investigation (sciences naturelles v. sciences sociales). Dans cette thèse, j'étudie plus spécifiquement la "biodiversité", qui se

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<sup>1</sup>Interdisciplinary Panel on Biodiversity and Ecosystem Services

<sup>2</sup>Voir le [communiqué de presse du rapport 2019](#)

<sup>3</sup>Traduit par l'auteur

concentre sur la variabilité des organismes vivants. Bien qu'il s'agisse d'un concept ambigu, la biodiversité tend à mettre l'accent sur les organismes vivants, en relation avec leur environnement matériel, biotique et abiotique (par opposition à l'étude de l'environnement non vivant) et sur son rôle essentiel parmi les autres composantes du système terrestre.

Le rapport de l'[IPBES \(2019\)](#) documente les changements drastiques que subit la biosphère et examine ces changements dans une optique anthropocentrique, c'est-à-dire en médiatisant les changements susmentionnés par les contributions multiples et diverses que la nature et la biodiversité apportent à l'homme. Il souligne l'impact de leur perturbation sur la vie humaine et met en évidence le rôle des facteurs anthropogéniques (c'est-à-dire d'origine humaine) dans la perturbation de la nature et de la biodiversité.

Ce rapport fixe différents objectifs à la recherche scientifique. Le premier objectif est d'expliquer les mécanismes de rétroaction : comment la vie de l'humanité influence-t-elle la biodiversité ? En réponse, comment la biodiversité influe-t-elle sur la vie de l'humanité ? Cet objectif implique, d'une part, de comprendre les causes et de mesurer les facteurs anthropiques directs et indirects de changement dans la nature et la biodiversité et, d'autre part, de comprendre les canaux et les échelles par lesquels la nature et la biodiversité contribuent aux moyens de subsistance de l'homme, ainsi que de mesurer ces contributions. Par conséquent, l'étude de la disparition de la nature et des possibilités d'y remédier nécessite une perspective intégrée, qui associe les sciences naturelles aux sciences sociales, par le biais de cadres tels que les systèmes socio-écologiques ([Ostrom, 2009](#)) ou l'économie environnementale et écologique ([Daly, 2007](#)).

Le deuxième objectif est de fournir un cadre pour évaluer l'opportunité, la faisabilité et les moyens de mise en œuvre des voies collectives qui permettraient de remédier à la crise à laquelle la nature est confrontée. D'une certaine manière, il s'agit de concevoir et de mettre en œuvre des voies politiques vers des avenir durables, c'est-à-dire de trouver des voies ou des méthodes d'action définies choisies parmi des alternatives, aux niveaux individuel, collectif ou gouvernemental, pour parvenir à des états futurs du monde qui restent dans un espace de fonctionnement sûr en ce qui concerne les limites planétaires ([Rockström et al., 2009; Steffen et al., 2015](#)).

Dans cette thèse, j'aborde ces deux objectifs en utilisant un cadre issu de l'économie et de l'écologie. Une première version des questions de recherche que cette thèse vise à résoudre est la suivante :

1. Quelles sont les relations de rétroaction entre la biodiversité et les facteurs anthropogéniques de son déclin ?
2. Quels sont les mécanismes sous-jacents auxquels les politiques doivent s'attaquer

pour remédier à ce déclin ?

3. Comment les approches économiques et écologiques intégrées peuvent-elles être utilisées et affinées pour analyser, informer et concevoir des politiques publiques?

Afin d'affiner ces questions, je commence par définir le concept de biodiversité, à travers ses évaluations en sciences naturelles et sociales, et je souligne les tendances actuelles de sa disparition.

## **Emergence et définition de la biodiversité comme concept écologique**

La biodiversité est apparue en tant que concept dans les années 1980, parallèlement à l'émergence de la "biologie de la conservation", une branche de la biologie qui s'intéresse à la protection de la "diversité biologique" (Soulé, 1985), en réponse à l'accélération de la disparition des espèces. La position morale de la biologie de la conservation est que les espèces doivent être protégées pour elles-mêmes (Soulé, 1986), elles ont une valeur intrinsèque. Le concept de biodiversité s'inscrit donc dans un jugement éthique et un appel à l'action. Dans le sillage de la conférence des Nations unies sur l'environnement et le développement qui s'est tenue à Rio en 1992, la [Convention sur la diversité biologique](#) s'est imposée comme un traité international visant à sauvegarder la biodiversité. Ce faisant, elle a fourni une définition internationalement reconnue :

*La "diversité biologique" désigne la variabilité des organismes vivants de toute origine y compris, entre autres, les écosystèmes terrestres, marins et autres écosystèmes aquatiques et les complexes écologiques dont ils font partie ; cela comprend la diversité au sein des espèces et entre espèces ainsi que celle des écosystèmes.*

[Article 2 de la Convention sur la Diversité Biologique<sup>4</sup>](#)

Cette définition met en évidence un élément clé de différenciation par rapport à d'autres parties de la nature, à savoir la nature vivante des objets étudiés. Par rapport aux facteurs abiotiques, la diversité biologique se caractérise par une croissance, une reproduction et un métabolisme intrinsèques (au niveau de l'individu et de la population), ainsi que par une évolution (au niveau de la génétique et de l'espèce). En outre, ces taux de changement dans le temps sont commensurables avec l'expérience humaine, et la plupart des processus (par exemple, la reproduction, l'effondrement ou la reconstitution des populations, l'évolution

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<sup>4</sup>Traduit par l'auteur

génétique) peuvent être observés au cours d'une vie humaine, par opposition à l'échelle temporelle géologique.

Comme le soulignent [Dyke and Lamb \(2008\)](#) et [Mouysset \(2023\)](#), la définition de la biodiversité est difficile, car elle recouvre des dimensions éthiques, conceptuelles et de mesure. La biodiversité peut être considérée comme "une qualité intrinsèque et sans mesure des systèmes naturels qui devrait être préservée pour elle-même" ([Dyke and Lamb, 2008](#); [Mouysset, 2023](#))<sup>5</sup>, mais elle se réfère également à des caractéristiques mesurables. Cette définition implique différentes échelles d'un point de vue hiérarchique, au niveau génétique, au niveau de l'espèce, de la communauté et de l'écosystème (défini comme l'interaction des communautés et de leur environnement abiotique). Ces niveaux impliquent différentes formes de mesure, notamment la distribution des gènes, l'abondance des espèces (le nombre d'individus dans une population, à un moment et à un endroit donnés), la richesse des espèces (le nombre d'espèces différentes, à un moment et à un endroit donnés) au sein des communautés, entre les communautés et à des échelles plus grandes (les diversités alpha, bêta et gamma), ainsi que les variations des facteurs abiotiques qui forment les écosystèmes, tels que la température, l'humidité, la qualité de l'eau, la qualité du sol, etc. Elle comprend également différents types de diversité : la diversité structurelle (par exemple, les couches de la canopée dans les forêts, le sex-ratio dans les populations animales), la diversité de composition (la variété et l'abondance des espèces au sein d'une communauté) et la diversité fonctionnelle (la variété des processus environnementaux réalisés par les organismes vivants dans une zone donnée, par exemple la séquestration du carbone, le cycle des nutriments ou la dispersion des graines, voir [Loreau et al. \(2002\)](#)).

[Mouysset \(2023\)](#) souligne la difficulté d'articuler la définition avec les niveaux communs de l'analyse scientifique, par exemple génétique, taxonomique et écosystémique, car le niveau de biodiversité peut se situer entre les deux : "les populations peuvent être considérées d'un point de vue génétique et taxonomique, ou les communautés qui se situent entre les niveaux taxonomique et écosystémique". En outre, la diversité structurelle et compositionnelle pouvant être considérées comme les sources de la diversité fonctionnelle, il peut être difficile de travailler avec les différentes classes de diversité en raison de leur colinéarité.

Les multiples dimensions de la biodiversité mettent en évidence plusieurs de ses caractéristiques essentielles. Tout d'abord, il est impossible de mesurer la biodiversité à l'aide d'un seul indicateur. L'étude de la biodiversité nécessite de multiples indicateurs pour évaluer de manière intégrée l'évolution de la biodiversité, à toutes les échelles et pour tous les types de diversité. L'émergence du concept répond à un désir de protéger la biodiversité pour son propre bien, mais

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<sup>5</sup>Traduction de l'auteur

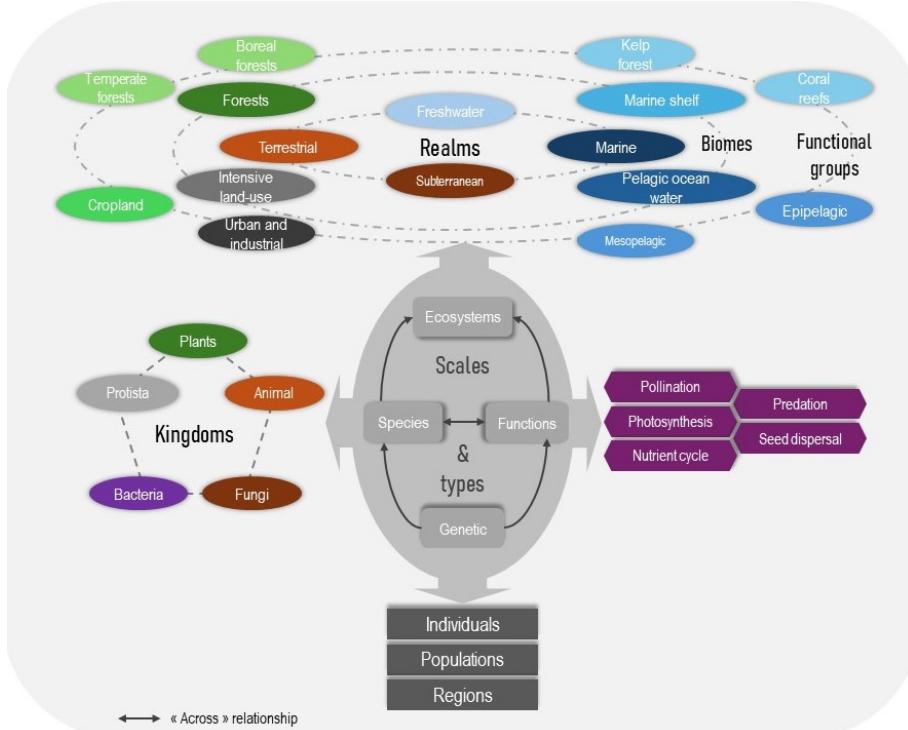


Figure 2: La biodiversité : un concept multiforme à travers échelles et types

aussi pour celui de l'humanité.

## Les Contributions de la Nature aux Populations : logiques de conservation de la biodiversité

D'abord descriptives, les fonctions des écosystèmes ont été de plus en plus considérées d'un point de vue humain à partir des années 1970 ([Hueting, 1969](#); [Schumacher, 1973](#)), évoluant vers le concept de services écosystémiques ([Ehrlich, 1981](#)) pour illustrer les conséquences de la perte de biodiversité ([Gómez-Baggethun et al., 2010](#)). Cette évolution a marqué le passage d'une valeur intrinsèque à une valeur anthropocentrique (c'est-à-dire donnée par l'homme) ([Mouysset, 2023](#)), reconnaissant les valeurs instrumentales et relationnelles de la biodiversité - servir les objectifs des humains et favoriser des relations significatives avec les autres et l'environnement. Progressivement, la biodiversité a dû être protégée pour son rôle dans le maintien de la vie humaine.

Le concept a fait son chemin dans la recherche universitaire, et lorsque [Costanza et al. \(1997\)](#) a quantifié la valeur du capital naturel et des services écosystémiques au stupéfiant montant de 33 trillions \$USD, soit environ 30% du PIB mondial de 2020, le concept est entré dans l'arène politique. En 2005, le Millennium Ecosystem Assessment ([Hassan et al., 2005](#)) a placé les services écosystémiques au centre de l'agenda politique : elle a souligné une valeur anthropocentrique des services écosystémiques, mais a établi une dépendance des sociétés humaines aux services

écosystémiques, et plus loin, au fonctionnement de l'écosystème. À cet égard, le Millenium Ecosystem Assessment ([Hassan et al., 2005](#)) a marqué un tournant dans la sauvegarde de la biodiversité par le biais d'un paradigme de soutenabilité forte (voir encadré 1), et a déclenché l'opérationnalisation du concept dans les politiques à grande échelle (ce que je développerai plus loin). Le cadre des services écosystémiques a été divisé en 4 catégories, liées au type spécifique de services contribuant au "bien-être humain" : les services de soutien (par exemple, les services permettant à d'autres services écosystémiques d'être présents, y compris le cycle des nutriments et la production primaire) et les services de régulation ("avantages obtenus par la régulation des processus écosystémiques", par exemple la pollinisation, la décomposition des déchets, la gestion de l'eau, etc.) ; les services culturels ("les avantages non matériels que les gens tirent des écosystèmes par l'enrichissement spirituel, le développement cognitif") et les services d'approvisionnement ("tous les produits tirés des écosystèmes",[Hassan et al. \(2005\)](#), p.54)

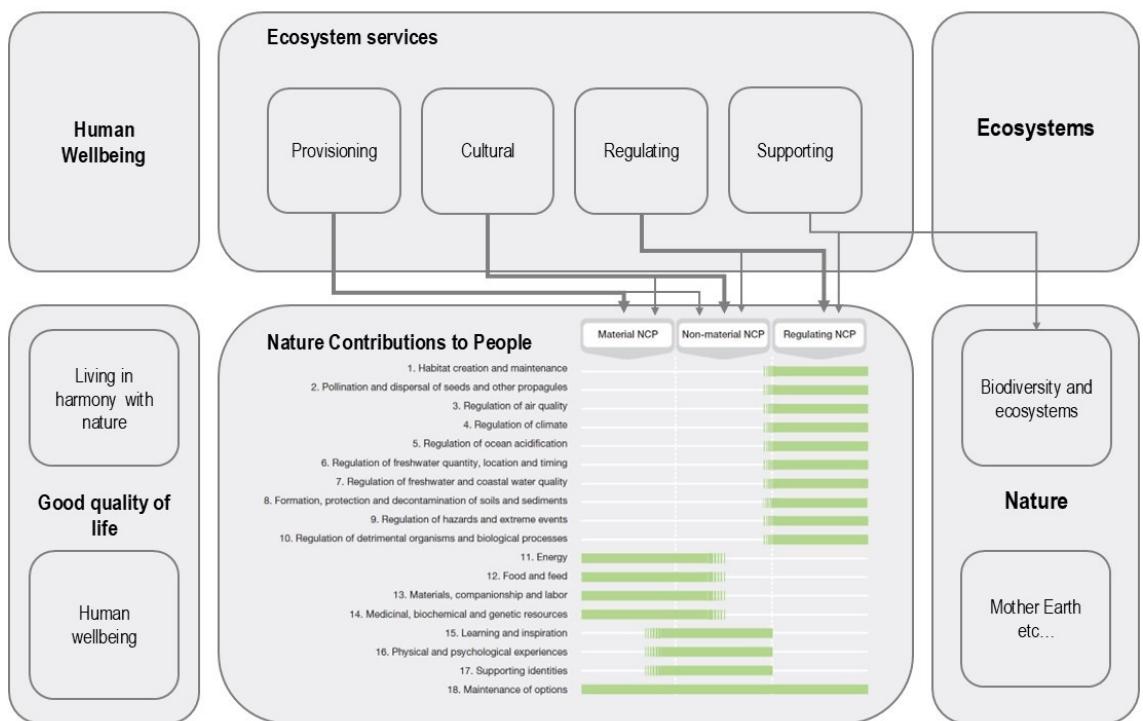


Figure 3: Description des 18 Contributions de la Nature aux Populations et du lien entre le cadre des CNP ([IPBES, 2019](#)) et le cadre des services écosystémiques ([Millennium Ecosystem Assessment, 2005](#))

Adapté depuis [Díaz et al. \(2018\)](#) et [IPBES \(2019\)](#)

Récemment, l'IPBES est passée à un nouveau cadre conceptuel mettant en évidence les contributions de la nature aux populations (CNP) ([Díaz et al., 2015](#)), définies comme "toutes les contributions, positives et négatives, de la nature vivante [...] à la qualité de vie des populations" ([Díaz et al., 2018](#)). Ce cadre soutient trois types de contributions aux personnes : les contributions matérielles

aux personnes (flux de la nature vers les personnes généralement consommés pour "faire fonctionner une société ou une entreprise" [IPBES \(2019\)](#), p.16), les contributions non matérielles (par exemple, les effets de la nature sur "les aspects subjectifs et psychologiques qui sous-tendent la qualité de vie des populations") et les contributions régulatrices (par exemple, "les aspects fonctionnels et structurels des organismes et des écosystèmes qui modifient les conditions environnementales vécues par les personnes et/ou régulent la génération de contributions matérielles et non matérielles"). Ce cadre met en évidence le fait que les contributions de la nature à l'homme peuvent être positives ou négatives et dépendent de la définition spatiale et temporelle de la contribution, puisqu'une entité donnée peut être à la fois la source de contributions positives et négatives : par exemple, les forêts favorisent l'habitat, mais risquent également de mettre en danger les personnes en cas d'incendies de forêt. En outre, elle offre une vision plus globale que les services écosystémiques, car elle englobe des perspectives allant de la biodiversité en tant que capital naturel utilisé dans une fonction de production écologique (voir [Polasky and Segerson \(2009\)](#) pour une revue), ainsi que des perspectives où la biodiversité a une agence et est liée par des obligations de soins réciproques envers les humains ([Descola, 2013](#)).

Une correspondance à multiples facettes entre les différentes composantes et dimensions de la biodiversité et ses contributions à l'homme est à la base des moyens de subsistance de l'homme. Le déclin mondial de la biodiversité menace les CNP.

### Box 1 - Soutenabilité Faible et Forte

En 1987, la publication du rapport Brundtland (WCED, 1987) a donné une définition large du développement durable :

*Par essence, le développement durable est un processus de changement dans lequel l'exploitation des ressources, la direction des investissements, l'orientation du développement technologique et les changements institutionnels sont tous en harmonie et améliorent le potentiel actuel et futur de satisfaction des besoins et des aspirations de l'humanité<sup>a</sup>*

WCED (1987), p.43

La mise en œuvre du développement durable est restée une question ouverte. En économie, une « perspective de durabilité faible », inaugurée par les travaux de Hartwick (1977) et Solow (1986) sur les ressources épuisables, suggérait que « le maintien d'un stock de capital non décroissant, qui pourrait être mis en pratique en investissant dans le capital manufacturé toutes les rentes dérivées de l'exploitation des ressources naturelles non renouvelables »<sup>b</sup> (Gómez-Baggethun et al., 2010) était suffisant pour maintenir la consommation au fil du temps. Dans cette approche, le capital naturel pouvait être intégralement remplacé par le capital humain. D'autre part, l'approche de la « durabilité forte » prône la complémentarité, plutôt que la substituabilité, des ressources naturelles (Costanza and Daly, 1992), reconnaissant ainsi la dépendance des humains à l'égard des écosystèmes.

<sup>a</sup>Traduit par l'auteur

<sup>b</sup>Traduit par l'auteur

## Déclin de la biodiversité : tendances et facteurs

Les mesures de la biodiversité diminuent à toutes les échelles d'analyse. Les conditions structurelles des écosystèmes, la composition des communautés écologiques et les populations d'espèces ont connu des changements spectaculaires. La part des habitats sauvages protégés et inchangés s'est effondrée sur terre et en mer (Watson et al., 2016; Jones et al., 2018) pour atteindre 23% et 12% de l'espace, respectivement. Au niveau des communautés, la part de la biodiversité initialement présente tombe en dessous de 90 % dans tous les biomes, (Hill et al., 2018) et les communautés locales deviennent de plus en plus semblables (McKinney and Lockwood, 1999), sous l'effet de l'augmentation de l'étendue des espèces exotiques envahissantes animales et végétales, en hausse de 13 % par décennie (Seebens et al., 2017). A ce jour, la richesse des espèces mondiales est menacée par une extinction massive, car le taux mondial d'extinction des espèces est au moins dix fois plus élevé que le taux moyen des 10 derniers millions d'années et s'accélère (Barnosky et al., 2011; Ceballos et al., 2015). En moyenne, 25 % des

espèces sont actuellement menacées d'extinction à l'échelle mondiale dans un large éventail d'espèces végétales et animales, sur terre et en mer ([International Union for the Conservation of Nature - IUCN, 2024](#)). En utilisant des méthodes fondées sur l'habitat, [Hoskins et al. \(2020\)](#)<sup>6</sup> constatent que des centaines de milliers d'espèces végétales et animales sont menacées et rembourseront la *dette d'extinction* causée par les changements anthropogéniques de leurs habitats : seulement 92,1% des espèces de vertébrés terrestres, 91,6% des invertébrés terrestres et 90,7% des plantes terrestres disposent d'un habitat suffisant pour subsister. Ces résultats suggèrent qu'environ un demi-million d'espèces animales et végétales terrestres - dont plus de 3 000 vertébrés et plus de 40 000 plantes - sont condamnées à s'éteindre, à moins que leurs habitats ne s'améliorent à temps pour l'empêcher ([IPBES, 2019](#)).

Les facteurs de déclin de la biodiversité sont d'origine anthropique. Ils peuvent être classés en deux catégories : les facteurs *directs*, qui découlent directement des actions humaines, comme le changement d'utilisation des terres, le changement climatique anthropique, la surexploitation, et les facteurs *indirects*, qui peuvent être considérés comme la cause première des facteurs directs, comme les changements dans les systèmes de valeurs qui sous-tendent les utilisations de la nature ([IPBES \(2019\)](#) p. 55), la démographie (urbanisation et migration), la technologie, l'économie (transitions sectorielles, expansion du commerce) et la gouvernance (y compris les systèmes de risque pour l'accès aux ressources).

Une synthèse des sciences naturelles réalisée par l'[IPBES \(2019\)](#) souligne le rôle des principaux facteurs à l'échelle mondiale et dans tous les biomes (voir figure 4). Il montre que le changement d'utilisation des terres et des mers, c'est à dire la perte, la fragmentation, et la dégradation de l'habitat<sup>7</sup> % L'exploitation

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<sup>6</sup>La liste rouge de l'IUCN utilise des comptes détaillés pour les espèces, dans une approche ascendante, afin d'analyser le risque d'extinction des espèces. Une approche descendante, qui s'appuie sur l'évolution de l'habitat disponible et la relation espèce-zone, utilise les changements dans l'utilisation des terres pour prévoir l'extinction des espèces de manière plus globale. ([Diamond, 1972](#))

<sup>7</sup>La perte d'habitat est sans aucun doute le principal moteur du déclin de la biodiversité terrestre. Les effets de la fragmentation sur la biodiversité sont très controversés. D'un point de vue théorique, des modèles ont été développés pour étudier l'évolution des populations et des communautés dans l'espace et le temps, par exemple les modèles de métapopulation et de métacommunauté. Les connaissances théoriques soulignent que la fragmentation de l'habitat augmente le risque d'extinction et réduit la probabilité de colonisation, ce qui se traduit par une baisse de la survie et de la diversité ([Adler and Nuernberger, 1994; Hill and Caswell, 1999; Thompson et al., 2017](#)). À l'échelle communautaire, l'augmentation de la diversité entre les communautés (par exemple, la diversité bêta) peut résulter des différentes exigences des espèces en matière de ressources et de la plus grande étendue spatiale, qui englobe donc une plus grande hétérogénéité environnementale, résultant de la fragmentation ([Lasky and Keitt, 2013; Chisholm et al., 2018](#)). Toutefois, ces effets s'atténuent à mesure que la perte d'habitat diminue. Au niveau empirique, l'effet de la fragmentation est très discuté. Selon [Fahrig \(2017\)](#), il n'existe aucune preuve empirique qu'un groupe de petites parcelles d'habitat a généralement une valeur écologique inférieure à celle de grandes parcelles de la même superficie totale. Des éléments montrent toutefois que la fragmentation ne réduit pas la connectivité des habitats, car la connectivité fonctionnelle est améliorée (par exemple, les espèces sont en contact avec un plus grand nombre de parcelles

directe de la faune et de la flore sauvages et la dégradation de l'habitat de la faune sont responsables de 30% des impacts sur la biodiversité. L'exploitation directe de la faune et de la flore sauvage représente 23 % des impacts. Le changement climatique, qui se traduit par des modifications des conditions biogéographiques et des changements d'habitat, a un impact sur les caractéristiques des espèces et l'évolution génétique, ce qui représente 14% des impacts, et la pollution représente 14% des impacts. Enfin, les espèces exotiques envahissantes représentent 11%. Ces facteurs ont des impacts différents selon les écosystèmes et les biomes ([IPBES, 2019](#)).

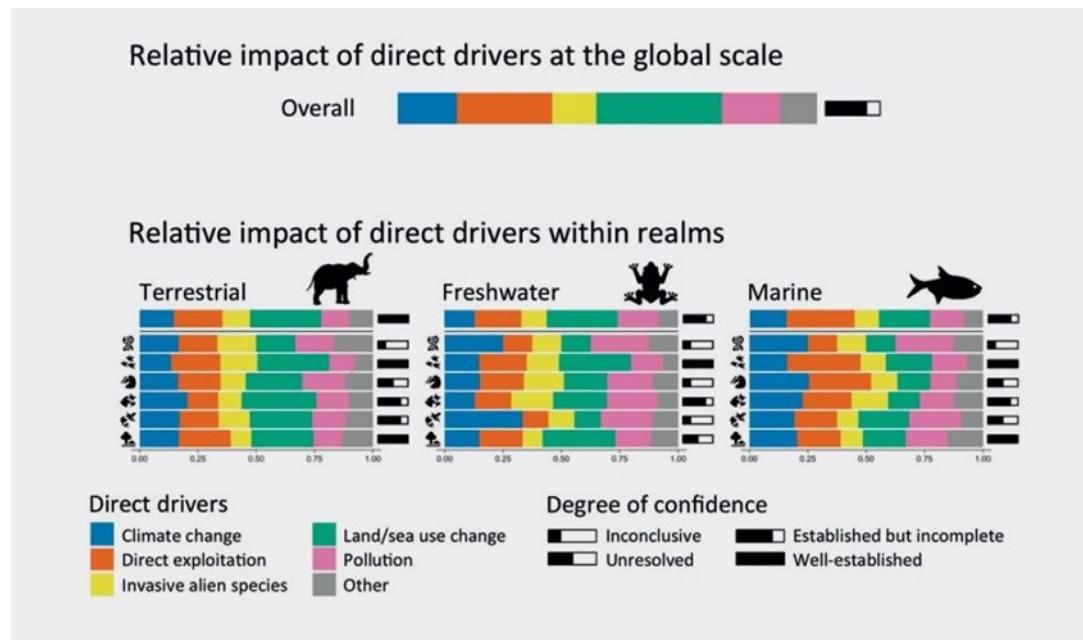


Figure 4: Effets agrégés et par biômes des impacts des moteurs anthropogéniques directs du déclin de la biodiversité, adapté de [IPBES \(2019\)](#)

Sur terre, le changement d'usage des terres est le facteur le plus important (30.5%), sous l'effet de la déforestation et de l'agriculture, suivi de l'exploitation directe (21%). Les forêts tropicales et subtropicales sèches et humides abritent la plus grande diversité biologique. Par exemple, elles abritent les 10 hotspots qui comptent le plus grand nombre de vertébrés ([Mittermeier et al., 2011](#)). Dans ces forêts, la perte et la dégradation de l'habitat sont les principaux facteurs de réduction de l'abondance et de la richesse des espèces ([Newbold et al., 2014](#)). L'exploitation forestière sélective légale et illégale détruit l'habitat ([Hoare and Uehara, 2022; Bousfield et al., 2023](#)) et est combinée à la chasse et au braconnage

de ressources différentes, ce qui améliore le fonctionnement global des écosystèmes). Le débat entre [Fletcher et al. \(2018\)](#) et [Fahrig et al. \(2019\)](#) porte sur les critiques fondées sur la capacité des modèles statistiques à englober l'effet de la fragmentation en cas de perte d'habitat ([Ruffell et al., 2016](#)). En outre, il reflète la difficulté de l'écologie paysagère, car différents mécanismes à travers les échelles, par exemple la parcelle, le paysage et la région d'étude, et des mesures, telles que la taille de la parcelle, l'isolement de la parcelle (par exemple la distance entre les parcelles) et la distance au bord de la parcelle (par exemple la distance au bord à l'intérieur de la parcelle) interagissent avec des interactions non linéaires possibles.

des espèces sauvages (Gallego-Zamorano et al., 2020), générant entre 60 et 180 milliards \$ USD de revenus (GFI, 2017)<sup>8</sup>.

Pour les espèces marines, la surexploitation est le principal moteur (29%) (IPBES, 2019). Avec 90 millions de tonnes de captures (et 141 milliards de dollars) en 2020 (FAO, 2022), les stocks halieutiques se situant à des niveaux biologiquement durables ont diminué pour atteindre 64,6% en 2019, contre 90% en 1974<sup>9</sup>, sous l'effet de la surpêche dans le Pacifique Sud-Est et dans les mers Méditerranée et Noire. Néanmoins, la pêche illicite, non déclarée et non réglementée (INN) constitue une menace pour les pêcheries. Selon des estimations datant d'il y a 15 ans (Agnew et al., 2009), elle représenterait entre 11 et 26 millions de tonnes de poisson pour une valeur de 10 à 23 milliards de dollars américains.

En outre, le changement climatique anthropique entraîne des perturbations des écosystèmes sur terre (Burrell et al., 2020; Conradi et al., 2024) et en mer (Gomes et al., 2024), par le biais de changements dans divers canaux , y compris l'adéquation des habitats et les perturbations du réseau trophique. Sur terre, par exemple, les forêts, bois et maquis méditerranéens, qui couvrent 4 millions de km<sup>2</sup>, sont des zones d'une diversité exceptionnellement élevée (Mooney et al., 2001; Blondel et al., 2010), menacées par l'expansion urbaine et l'augmentation du risque d'incendie de forêt. La fréquence et la gravité des incendies de forêt devraient augmenter avec le réchauffement climatique (Dupuy et al., 2019), entraînant d'importants coûts directs et indirects pour la société , notamment la destruction d'infrastructures et des perturbations de l'activité économique (Wang et al., 2021), les problèmes de santé liés à la fumée (Burke et al., 2023; Heft-Neal et al., 2023), la perturbation des caractéristiques structurelles des écosystèmes (Ayars et al., 2023) et la menace pour la diversité biologique (Wintle et al., 2020).

## Défis économiques des facteurs anthropogéniques du déclin de la biodiversité

La perte d'habitat et la surexploitation présentent des défis à la fois communs et différenciés. Une cause commune identifiable est le coût d'opportunité élevé de la préservation de l'habitat ou de l'existence d'une espèce, en présence d'autres alternatives économiques pour la terre et le temps, ainsi que de contraintes financières. En outre, la perte d'habitat et la surexploitation partagent un aspect dynamique temporel, où les actions immédiates ont des conséquences durables, voire irréversibles.

La perte et la fragmentation de l'habitat dans les écosystèmes terrestres posent

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<sup>8</sup>Le commerce illégal d'espèces sauvages représente entre 5 et 23 milliards \$USD, tandis que l'exploitation forestière illégale représente entre 52 et 157 milliards \$USD

<sup>9</sup>Dans ce calcul, tous les stocks halieutiques sont pris en compte de la même manière, indépendamment de leur abondance ou de leurs captures

des problèmes spécifiques. Les forêts, par exemple, ont des usages multiples (ou CNP) pour différents agents : les bûcherons tirent profit du bois, certains défrichent les terres pour l'agriculture, les randonneurs recherchent des paysages vierges et les défenseurs de l'environnement visent à rétablir les cycles naturels. Les forêts ont également une valeur spirituelle et culturelle. Ces différents usages rentrent donc en conflit. Par exemple, la déforestation et l'urbanisation détruisent à la fois l'habitat et les terres sacrées, mais créent une valeur économique mesurée ([Giglio et al., 2024](#)), tandis que la prévention des incendies de forêt peut endommager l'habitat des espèces sauvages ([Bradshaw et al., 2018](#)). Les espèces peuvent également avoir des impacts mixtes ; les cerfs, par exemple, sont appréciés à faible densité mais causent des dommages à des densités plus élevées ([Putman et al., 2011](#)). Le changement climatique aggrave la perte d'habitat en modifiant la distribution des habitats et en augmentant les menaces telles que les incendies de forêt ([Dupuy et al., 2019; Wasserman and Mueller, 2023](#)). Une deuxième caractéristique essentielle pour mettre fin à la fragmentation des habitats est la prise en compte de l'ensemble des interdépendances, des retombées écologiques et des externalités économiques qui sous-tendent la dimension spatiale. La configuration de l'espace et le mouvement des espèces sont, au moins en partie, le résultat d'une décision économique. Le maintien de la connectivité des habitats passe par l'identification des parcelles et des chemins à conserver ou à restaurer qui y contribuent le plus, sous forme de corridors, d'écoducs ou de trempins ([Turner, 2005; Turner and Gardner, 2015](#)). La valeur des parcelles et des chemins pour la connectivité est intrinsèquement liée à leur environnement : au même endroit géographique, une parcelle a une valeur différente pour l'habitat de la biodiversité si elle est connectée à d'autres, ou si elle est isolée (voir encadré 2). Lorsque les chemins échappent au contrôle de l'homme, les parcelles ont une importance différente en fonction de leur emplacement, et lorsque l'emplacement des parcelles est fixe, l'étendue des chemins et leur emplacement sont primordiaux.

Troisièmement, lorsque des actions et des utilisations multiples structurent des éléments connectés des écosystèmes (par exemple, différentes étendues de terre ou différentes échelles de biodiversité), elles entraînent des retombées spatiales, c'est-à-dire des conséquences qui vont au-delà de leurs effets *in situ*, avec des répercussions dans la durée. Lorsque ces retombées ne sont pas prises en compte par les agents qui les génèrent, elles peuvent être appelées « externalités spatiales dynamiques » ([Sanchirico and Wilen, 1999; Costello and Polasky, 2008; Costello et al., 2017](#)). Étant donné que l'arrêt de la perte et de la fragmentation des habitats implique la conservation de parcelles de terre, les parties voisines peuvent très bien bénéficier (ou souffrir) d'un plus grand nombre d'espèces sauvages et de (dis-)services écosystémiques sur leur propriété, au fil du temps. Comme les agents réagissent aux profils d'action des autres, ils adoptent un comportement

ment stratégique, à la fois dans l'espace et dans le temps. Ces externalités peuvent déclencher des problèmes spécifiques de " cercle vicieux" (Costello et al., 2017) : lorsque les parties voisines d'un décideur qui entreprend la conservation, ou la réduction des risques, ne se rendent pas la pareille alors qu'elles bénéficient des retombées, un cercle vicieux de moindre action est déclenché. Inversement, lorsque les retombées écologiques sont positives, cela peut conduire tout le monde à utiliser une ressource à des niveaux non durables, même en présence de droits bien définis, en l'absence d'autres mécanismes (Janmaat, 2005; Kaffine and Costello, 2010). Par conséquent, la fragmentation de l'habitat et la surexploitation sont liées par la connectivité spatiale.

Quatrièmement, arrêter la perte et la fragmentation des habitats implique de coordonner de nombreux acteurs en vue d'accroître la superficie et la connectivité des habitats, tout en tenant compte des coûts et des avantages associés, ainsi que des différents intérêts. Dans certains cas, les contraintes financières, l'ampleur des coûts associés à l'augmentation de la connectivité des habitats et la difficulté de la coordination justifient une politique publique dans laquelle un planificateur central entreprend l'action (Mouysset et al., 2012). D'autre part, il existe des mécanismes permettant de décentraliser une planification spatiale efficace, qui peuvent être efficaces lorsque les coûts de coopération sont limités (Costello et al., 2017; Bareille et al., 2023).

Pour mettre un terme à la surexploitation, il faut comprendre et traiter ses motivations. La surexploitation (ou le sous-contrôle, pour les espèces nuisibles) résulte d'un déséquilibre entre l'appropriation et l'utilisation des contributions de la nature aux populations (tant positives que négatives) et le niveau et la répartition socialement souhaitables de ces contributions, ainsi que du comportement stratégique non coordonné des agents. La nature commune de la plupart des ressources naturelles (Gordon, 1954; Smith, 1969) a longtemps été identifiée comme l'une des principales raisons de leur disparition : de nombreux événements ont montré eux aussi des dynamiques de cercles vicieux, de tragédie des communs (Hardin, 1968), où l'absence de droits de propriété sûrs a accéléré la surexploitation et le déclin des populations. Cette question est depuis longtemps au centre de l'attention, et les mécanismes reposant sur l'attribution de droits de propriété ont fait l'objet d'études approfondies (Libecap, 2009; Costello et al., 2015; Isaksen and Richter, 2019).

## Encadré 2 - Habitat : perte, fragmentation et connectivité

La perte d'habitat correspond à la perte de zones présentant des conditions environnementales adéquates pour la survie et le développement des espèces. À surface d'habitat constante, la fragmentation se traduit par une augmentation du nombre de parcelles et une diminution de la taille moyenne de chaque parcelle, comme le montre la figure 5.

La connectivité du paysage est définie par rapport à la fragmentation. Elle mesure "le degré auquel le paysage facilite ou entrave le mouvement entre les parcelles de ressources" (Taylor et al., 1993). Elle recouvre une dimension *structurelle*, qui décrit les arrangements physiques entre les parcelles, et une dimension *fonctionnelle*, qui met l'accent sur la capacité et la réalisation des mouvements des individus à travers le paysage. Les mesures de connectivité globale tiennent compte du rôle des parcelles et des chemins différenciés. Dans le panneau D de la figure 5, les parcelles encerclées jouent un rôle déterminant dans le maintien de la connectivité. Les parcelles d'habitat 1 et 2 ont le même nombre de parcelles connectées. Cependant, la parcelle 1 maintient la connexion entre les parcelles d'habitat situées à l'est et à l'ouest du paysage et est reliée à des parcelles fortement connectées. La suppression des parcelles d'habitat 1 et 2 aurait des conséquences plus importantes sur l'habitat que la suppression d'autres parcelles de taille identique. De même, la suppression du chemin en pointillé (en bas à gauche du panneau D) isolerait la parcelle 3, tandis que la suppression du chemin en pointillé ne laisserait pas la parcelle 4 isolée. Par conséquent, les chemins et les îlots ont des impacts différents sur la connectivité, en fonction des îlots et des chemins environnants.

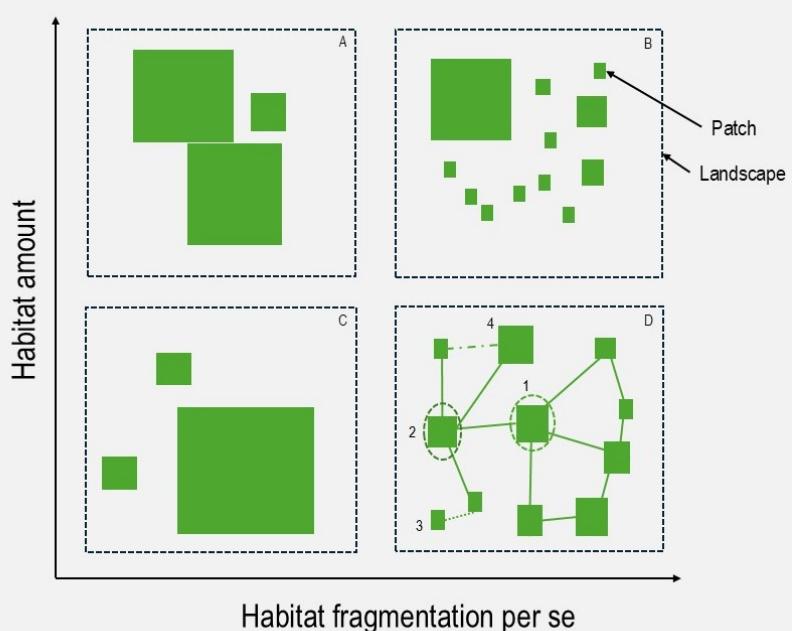


Figure 5: Illustration des effets de la perte d'habitat et de la fragmentation , adapté de Fahrig et al. (2019), ainsi que des effets de la connectivité

Toutefois, si les droits de propriété peuvent être attribués, il est notoirement difficile de les faire respecter dans les régions où les fonctions régaliennes sont contestées: des droits *de facto*, et non *de jure* sont attribués et appliqués. Dans ce cas, la nature commune de la ressource peut ne pas être la principale préoccupation: les forces locales de concentration du marché peuvent l'emporter sur les forces de surexploitation, même en présence d'une certaine forme d'accès libre ([Damania and Bulte, 2007](#)). Dans le monde entier, le braconnage et le commerce d'espèces sauvages sont généralement le fait de groupes criminels organisés et sont associés à différentes activités criminelles ([Mozer and Prost, 2023](#)). Des marchés concentrés tendent à émerger et à caractériser les marchés des espèces sauvages, car la concurrence est entravée par des groupes criminels organisés violents. Dans ce cas, la gestion des ressources est stratégique et répond aux caractéristiques du marché (structure de la demande, prix des marchandises intermédiaires) et aux caractéristiques écologiques (distribution des espèces, taux de croissance biologique, capacité de charge<sup>10</sup>) À un extrême, une structure de marché monopolistique locale pour les produits de la faune sauvage peut émerger, en particulier dans le cas d'espèces endémiques (par exemple, indigènes et limitées à une zone). Un monopole peut être le meilleur ami des défenseurs de la nature ([Solow, 1974; Hannesson, 1983](#)), en fonction des caractéristiques spécifiques du marché et des espèces, qui dépendent du contexte, car un monopole a intérêt à restreindre l'offre pour augmenter les prix, si les consommateurs ne réagissent pas trop (par exemple, en cas d'élasticité limitée de la demande). Un large éventail de structures de marché ([Damania and Bulte, 2007; Hannesson, 1985](#)) appliquées à des situations réelles a été étudié. Cependant, l'ensemble des interactions entre l'endémisme d'une espèce, le pouvoir de marché local, le coût de l'effort et l'accès aux marchés de consommation finale nécessite une analyse plus approfondie afin de clarifier l'impact de la structure du marché.

D'autres facteurs de surexploitation peuvent être trouvés dans les bénéfices importants attendus (par rapport à d'autres activités économiques locales) que certaines ressources naturelles peuvent supporter, la plupart du temps en raison de leur rareté (par exemple, l'absence de substitut économiquement viable), que ce soit aujourd'hui ou à l'avenir ([Kremer and Morcom, 2000](#)). Alors que les effets de la substitution de produits fabriqués par l'homme aux services écosystémiques perturbés commencent à faire l'objet d'études empiriques ([Frank, 2024](#)) et montrent à quel point les coûts peuvent être redoutables, l'effet de l'introduction de substituts aux produits de la faune sauvage braconnés illégalement peut être un exemple de substituabilité forte entre les actifs naturels et artificiels ([Chen, 2017](#)). Comme des forces plus larges affectent la surexploitation, y compris la pauvreté,

<sup>10</sup>La notion de *capacité de charge* est utilisée depuis le milieu du XXème siècle par les écologistes des populations (pour un historique de la notion, voir [Sayre \(2008\)](#)) pour décrire la taille maximale de la population d'une espèce qu'un écosystème donné peut supporter à long terme

il est clair que le traitement de la surexploitation implique de généraliser le raisonnement portant sur l'interaction d'une seule espèce avec le cadre institutionnel, comment l'avenir d'une espèce interagit avec la disponibilité des substituts, et comment la distribution des revenus provenant des récoltes durables peut favoriser une utilisation raisonnable de la ressource.

Un large éventail de politiques a été mis en œuvre à différents niveaux organisationnels, afin d'enrayer, conjointement ou séparément, les facteurs identifiés de déclin de la biodiversité sur terre et en mer, avec plus ou moins de succès.

## Politiques publiques de la biodiversité : du global au local

Les cadres politiques internationaux successifs ont cherché à enrayer la perte de biodiversité en s'attaquant à ses facteurs de manière globale. En 2022, la 15e conférence de la Convention des Nations unies sur la diversité biologique a lancé le [Keunming Montreal Global Biodiversity Framework \(GBF\)](#), remplaçant le Plan stratégique pour la biodiversité 2011-2020 et les Objectifs d'Aichi après avoir échoué à atteindre ses objectifs<sup>11</sup>. Le GBF fixe quatre objectifs mondiaux pour 2050, avec 23 objectifs mesurables pour stopper la perte de biodiversité d'ici 2030. Ces objectifs comprennent le maintien de l'intégrité et de la connectivité des écosystèmes et la prévention des extinctions induites par l'homme (objectif A), l'utilisation durable de la biodiversité (objectif B), le partage équitable des avantages et des charges liés à la conservation (objectifs C et D)<sup>12</sup>. Les objectifs comprennent la restauration de 30% des écosystèmes dégradés, la conservation de 30% des zones terrestres et marines et la garantie de l'utilisation et de la gestion durables des espèces sauvages.

D'autres traités internationaux, tels que la [Convention sur le commerce international des espèces de faune et de flore sauvages menacées d'extinction \(CITES\)](#) établie en 1973, réglementent le commerce des espèces menacées d'extinction afin d'empêcher le commerce illégal des espèces sauvages<sup>13</sup>. Malgré sa portée,

<sup>11</sup>Parmi les 20 Objectifs d'Aichi, aucun n'a été atteint au niveau mondial en 2020, et seulement 6 ont été partiellement atteints , y compris l'identification et l'éradication des espèces envahissantes sur les îles, la désignation de 17% des zones terrestres et des eaux intérieures et de 10% des zones côtières et marines comme zones de conservation, la mise en œuvre d'instruments politiques et d'une stratégie et d'une planification nationales efficaces en matière de biodiversité, et l'augmentation du financement de la protection de la biodiversité. Les raisons invoquées pour cet échec sont l'absence d'indicateurs clairs pour évaluer les objectifs, et l'absence d'obligation de rendre compte des progrès accomplis dans la réalisation des objectifs ([Maron et al., 2021](#))

<sup>12</sup>Voir [Section G. Keunming Montreal Global Biodiversity Framework pour 2050](#)

<sup>13</sup>CITES compte 183 parties membres (pays), elle répertorie les espèces à travers des « annexes », avec différents degrés de protection des espèces et des restrictions limitant le commerce des espèces menacées d'extinction.

Annexe 1 : les espèces les plus menacées, menacées d'extinction et dont le commerce international est interdit, sauf lorsque l'objectif des exportations n'est pas commercial.

Annexe 2 : espèces qui ne sont pas nécessairement menacées d'extinction à l'heure actuelle, mais

l'efficacité de la CITES est discutée. L'application du droit et la police au niveau local (Heid and Márquez-Ramos, 2023) et les campagnes de réduction de la demande (MacFarlane et al., 2022; Moorhouse et al., 2024) sont essentielles, mais les interdictions commerciales peuvent parfois augmenter les prix et les incitations au braconnage (Hsiang and Sekar, 2016). Dans certains cas, l'élevage de conservation a réussi à "inonder le marché" (Gentry et al., 2019; Phelps et al., 2014; Tensen, 2016). Les interventions du côté de l'offre ont parfois permis de réduire le braconnage et de reconstituer des populations sauvages - par exemple, la vigogne et le chat tacheté (IUCN, 2000; Sahley et al., 2007)- mais elles ont également échoué - par exemple, le python vert, l'éléphant d'Afrique (Lyons and Natusch, 2011; Hsiang and Sekar, 2016). L'incertitude quant aux résultats des approches fondées sur le marché en matière de conservation a conduit à continuer de s'appuyer sur des interdictions et des contrôles du commerce qui sont souvent inefficaces pour réduire le braconnage.

Les politiques nationales et supranationales ont également joué un rôle clé. Aux États-Unis, des politiques telles que *Wilderness Act of 1964* ont créé des zones protégées pour préserver les habitats. Dans le sillage du mouvement environnementaliste des années 1960 et 1970, des réglementations historiques visant à protéger les habitats naturels, telles que la *Clean Water Act de 1972* (garantissant que les eaux usées limitent la perturbation de l'habitat des espèces sauvages), et visant spécifiquement la conservation des espèces avec la *Endangered Species Act de 1973*. Les résultats de l'*Endangered Species Act* font l'objet d'un débat. Si les impacts semblent globalement positifs sur le rétablissement des espèces, le budget consacré aux inscriptions des espèces sur la liste des espèces en danger est mince, et les coûts associés sont substantiels et concentrés sur les propriétaires privés alors que les bénéfices sont plus largement répartis (Brown and Shogren, 1998; Langpap et al., 2018). Des initiatives locales, telles que le *Yellowstone Yukon Conservation Initiative* (1993), relient des zones écologiques à travers les États-Unis et le Canada, en utilisant des programmes de conservation privés et l'élaboration de politiques locales.

En Europe, le réseau Natura 2000<sup>14</sup> a créé la plus grande zone de conservation au monde, couvrant 18 % des régions terrestres et 9 % des régions marines de l'UE, à travers 28 000 sites. Dans les grandes lignes, elle délimite des zones de conservation d'intérêt écologique où le développement et les activités humaines sont limités. Son ambition était de prendre en compte l'échelle des processus

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qui pourraient le devenir si le commerce n'est pas étroitement contrôlé.

Annexe 3 : espèces inscrites à la demande d'une Partie qui réglemente déjà le commerce de l'espèce et qui a besoin de la coopération d'autres pays pour prévenir l'exploitation non durable ou illégale et promouvoir la survie de l'espèce.

<sup>14</sup>Un système de zones protégées, établi en application de la directive Oiseaux (1976) et de la directive Habitats (1992) de l'Union européenne, et officiellement mis en place à partir du milieu des années 2000

de la biodiversité plutôt que les frontières administratives pour développer un réseau inter-connecté de zones de conservation. Les performances écologiques et économiques d'un tel réseau sont considérables, car elles génèrent des retombées spatiales à la fois en termes de performances économiques et écologiques (Cocco et al., 2023).

Reconnaissant que l'habitat de la biodiversité peut être considéré comme un continuum entre des conditions inappropriées et appropriées, des mécanismes tels que les paiements pour services écosystémiques (PSE) sont mis à profit pour encourager la conservation sur les terres agricoles. En tenant compte des retombées écologiques de la diminution des retombées, les paiements pour les services écosystémiques assortis de primes d'agglomération, de sorte que les voisins bénéficient d'un avantage marginal supplémentaire lorsqu'un nouveau participant local met en œuvre des mesures de conservation, peuvent être efficaces (Parkhurst et al., 2002; Bareille et al., 2023). Dans l'ensemble, les conséquences spatiales des politiques décentralisées n'ont pas encore été pleinement intégrées dans l'élaboration des politiques.

Enfin, certaines politiques visent à atténuer les menaces que le changement climatique fait peser sur les écosystèmes et les espèces, en modifiant la connectivité des paysages. Dans les forêts méditerranéennes, où la biodiversité est exceptionnellement élevée mais où les incendies de forêt constituent une menace croissante (Dupuy et al., 2019; Wasserman and Mueller, 2023), les opérations de traitement des combustibles<sup>15</sup> pour limiter l'occurrence et la gravité des incendies de forêt. Les politiques publiques sont mises à profit pour faire face à l'augmentation des risques, à la limitation de l'assurabilité et aux menaces qui pèsent sur la biodiversité. Par exemple, l'assurabilité limitée des habitations situées à l'interface urbaine de la forêt en Californie<sup>16</sup>, ainsi que les dommages humains et non humains potentiels des incendies de forêt à l'échelle de l'économie (Wang et al., 2021; Heft-Neal et al., 2023; Ayars et al., 2023), les politiques de traitement des combustibles mandatées et gérées par l'État sont essentielles. Cependant, avec des budgets plus importants et un meilleur aménagement du territoire, ces poli-

<sup>15</sup>L'éclaircissement mécanique, les brûlages dirigés et, parfois, l'exploitation forestière, ont été mis à contribution pour réduire la charge de combustible dans les zones à risque et, théoriquement, pour diminuer la probabilité et la gravité des brûlures en cas d'incendie de forêt. Dans de nombreuses régions, telles que les forêts de conifères de Californie (Vaillant et al., 2009; Kalies and Yocom Kent, 2016; Low et al., 2023), les forêts d'eucalyptus du sud-ouest de l'Australie (Burrows and McCaw, 2013; Boer et al., 2009; Florec et al., 2020), le sud de l'Europe (Fernandes et al., 2013), il est prouvé que les traitements des combustibles peuvent atténuer l'intensité et la propagation des incendies de forêt. Les agences de gestion des terres ont historiquement mis en œuvre ces politiques en Australie (Burrows and McCaw, 2013), en Europe et aux États-Unis (et devraient s'intensifier, par exemple dans le cadre de l'Infrastructure Investment and Jobs Act de 2021 aux États-Unis)

<sup>16</sup>Par exemple, 200 000 propriétaires verront une augmentation de leur prime d'assurance de 34,1% en moyenne de la part de la compagnie d'assurance Allstate en novembre 2024. En 2023, le plan FAIR, conçu pour être l'assureur de dernier recours en Californie (mandaté par l'État mais financé par le secteur privé) a connu une augmentation de 38,3 % de son exposition totale.

tiques pourraient atteindre de meilleures performances en matière de réduction des risques tout en protégeant la biodiversité.

Des mécanismes politiques décentralisés existent, tels que des mandats pour créer une zone tampon défendable autour des propriétés individuelles: en Californie, une zone défendable de 100 pieds autour des maisons est obligatoire dans les zones de responsabilité de l'État, et peut se traduire par des primes d'assurance réduites; en France, dans les régions dédiées, l'obligation de débroussaillement impose des opérations de contrôle des combustibles dans un rayon de 50 m pour "diminuer l'intensité des incendies de forêt et limiter leur propagation"<sup>17</sup> avec des amendes pouvant atteindre 5 000 euros en cas de non-respect.

Dans le cadre de cette thèse, je me concentre sur l'analyse de l'interaction entre la biodiversité et les actions humaines, à travers les CNP qu' elle fournit et les moteurs anthropogéniques de son déclin. Étant donné que les politiques existantes ont eu des degrés de réussite variables dans l'arrêt de ce déclin, un cadre pour l'élaboration des politiques est nécessaire. J'utilise des méthodes issues de l'écologie et de l'économie pour analyser conjointement les causes de ce déclin et fournir des recommandations politiques publiques.

## Faire l'économie de la biodiversité

La définition de l'économie s'est élargie avec l'essor de nouvelles méthodes et de nouveaux objets, mais elle se concentre principalement sur l'analyse du comportement humain aux niveaux individuel et collectif afin de gérer des ressources limitées au travers de choix entre des alternatives exclusives ([Mankiw, 2011](#); [Bade and Parkin, 2002](#); [Backhouse and Medema, 2009](#)). Cela conduit à deux objectifs, en tant que champ de connaissance: comprendre et expliquer l'état du monde (approche positive) et déterminer les meilleures façons de gérer les ressources (approche normative). L'économie fournit donc des outils pour analyser les ressorts économiques de la perte de biodiversité et concevoir des politiques publiques permettant d'y remédier.

L'application de l'économie à la biodiversité est cependant un défi. Elle nécessite la mise en commun des valeurs, souvent par le biais d'une évaluation monétaire. Initialement, la biodiversité était évaluée pour ses produits (chasse, pêche, exploitation forestière) échangés aux prix du marché, en se concentrant sur les ressources dans un état spécifique - mortes. Cette approche ne prenait en compte qu'une partie de la « valeur d'usage » des espèces (dans le cadre des CNP, les contributions matérielles associées à la nourriture et aux matériaux), sans tenir compte de leur "valeur totale" ([Krutilla, 1967](#)). Au fil du temps, la notion de "valeur d'usage" s'est élargie pour inclure les contributions directes et indirectes

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<sup>17</sup>Translated by the author - Article L131-10 du Code Forestier

des espèces. De nombreuses études ont utilisé des prix de marché pour estimer la valeur de la biodiversité<sup>18</sup>. Lorsque les indicateurs de marché échouent, par manque de données par exemple, des techniques d'évaluation non marchandes ont vu le jour (Carson, 2012), s'appuyant sur les préférences déclarées<sup>19</sup>(mesurant des volontées de payer déclarées plutôt qu'observées).

Avec le cadre des services écosystémiques, les techniques d'évaluation monétaires ont été appliquées à grande échelle pour capturer divers services (Costanza et al., 1997), y compris les efforts récents de modélisation globale (Giglio et al., 2024). De multiples méthodes ont permis d'étendre l'évaluation de la biodiversité à toutes les échelles, de la génétique aux habitats et aux fonctions (Bartkowski et al., 2015).

Récemment, l'analyse s'est détournée des mesures monétaires directes pour évaluer les effets des espèces sur des résultats tels que la santé (Frank and Sudarshan, Forthcoming; Frank, 2024). Un nombre important de recherches ont rejeté l'évaluation monétaire, se concentrant plutôt sur des mesures de la biodiversité à mettre en balance avec les résultats économiques (Mouysset et al., 2011; Wätzold et al., 2016). Ces mesures permettent d'évaluer ou de planifier l'évolution de la biodiversité en lien avec ses mesures scientifiques, plutôt que sa valeur incomplète.

La gestion de la biodiversité implique de gérer des choix alternatifs pour ses usages et les éléments qui sous tendent son existence tout en prenant compte de la spécificité des éléments vivants, de leur taux de régénération et d'extinction, ce qui nécessite de comprendre sa dynamique temporelle. L'économie fournit un cadre pour modéliser cette dynamique et évaluer l'impact de différentes actions sur la biodiversité actuelle et future. Les modèles, en tant qu'"histoires structurées" ((Gibbard and Varian, 1978)), où la structure est "la forme logique et mathématique d'un ensemble de postulats" avec des "éléments d'interprétation" ((Gibbard and Varian, 1978)), sont utilisés à diverses fins (voir l'encadré 3).

Parallèlement à l'évolution des techniques d'évaluation monétaire, des modèles dits "bioéconomiques" ont été élaborés pour concevoir des politiques de gestion des ressources et de conservation de la biodiversité.

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<sup>18</sup>Par exemple, les méthodes hédoniques (Rosen, 1974) utilisent les variations des prix du marché pour des biens tels que l'immobilier liés aux caractéristiques environnementales, tandis que la méthode des coûts de voyage (Clawson and Knetsch, 1967; Bhandari and Heshmati, 2010) mesure les dépenses des consommateurs pour des expériences telles que l'observation de la faune et de la flore.

<sup>19</sup>Par exemple, à la suite de la marée noire de l'Exxon-Valdez en 1989, des enquêtes ont été mises au point pour estimer la valeur des ressources naturelles affectées, en demandant aux gens le montant qu'ils seraient prêt à payer pour sauver la vie d'un animal (car, 1992; Arrow et al., 1993; Carson et al., 2003), bien que ces méthodes soient controversées (Diamond and Hausman, 1994)

### Box 3 - Que font les modèles?

Varenne (2014) approfondit l'approche des modèles en tant que "médiateurs" entre le monde et l'analyse, et qualifie les modèles de "facilitateurs", à travers de multiples dimensions. Une typologie non exhaustive des rôles que peuvent jouer les modèles comprend (i) un rôle pédagogique (faciliter la communication), (ii) un rôle prédictif (faciliter l'anticipation), (iii) un rôle heuristique (faciliter l'explication d'un mécanisme avec quelques interactions simples), (iv) prescriptif (faciliter la réponse à un problème donné) et (iv) intégratif (faciliter les échanges entre disciplines).

## La modélisation bioéconomique pour l'analyse et la gestion de la biodiversité

Les modèles bioéconomiques sont des outils analytiques (c'est-à-dire avec une formulation mathématique) qui modélisent conjointement les rétroactions entre les composantes de la biodiversité dans les écosystèmes sauvages ou faiblement gérés, et les activités économiques à différents niveaux (par exemple, les niveaux micro, mezzo et macro). Ils combinent un modèle de décision issu de la théorie économique et la dynamique des éléments de la biodiversité issus de l'écologie. Les modèles bioéconomiques (Gordon, 1954; Smith, 1969; Clark, 1973) sont nés d'efforts conjoints d'économistes et d'écologues pour gérer les ressources en tenant compte de la dynamique spécifique des éléments biotiques (Parent et al., 2024)<sup>20</sup> en tant que modèles véritablement interdisciplinaires (voir l'encadré 4).

Historiquement, les premiers modèles bioéconomiques sont nés de l'écologie des populations et de l'analyse économique statique, pour étudier la gestion des pêches. Le modèle de Gordon-Schaeffer (Gordon, 1954; Schaefer, 1954) met en évidence l'évolution d'une population de poissons en fonction de différents régimes d'exploitation, et vise à maximiser les revenus à l'équilibre. Il distingue les niveaux d'effort entre ceux qui fournissent le rendement économique maximal (c'est à dire le profit économique maximal) et ceux qui fournissent le rendement durable maximal (la croissance la plus importante de la ressource halieutique), ce qui ouvre de nouvelles perspectives de gestion: étant donné que l'effort de rendement durable maximal est plus important que le rendement économique maximal, l'objectif devrait être ce dernier. Viser l'effort économique maximal permettrait d'obtenir des populations de poissons plus importantes et de promouvoir

<sup>20</sup>Comme le souligne (Parent et al., 2024), la concavité de la "fonction de production écologique", c'est-à-dire la concavité des débarquements de pêche résultait de l'application de la loi des rendements décroissants de l'effort de pêche. Ce n'est qu'avec l'apport de Schaeffer que la concavité de la fonction de production écologique dans Gordon (1954) a été fondée d'un point de vue écologique, à partir d'un argument de dynamique des populations (en utilisant une fonction de croissance logistique)

l'efficacité économique, par rapport à l'accès libre et non réglementé. Le modèle original a ensuite été étendu pour tenir compte de la dynamique transitoire et intégrer des éléments de la théorie du capital, en mettant l'accent sur l'allocation dynamique des ressources dans le temps (Smith, 1969; Clark, 1973).

Dans les années 1970, la prise de décision économique a été appliquée à la progression des parasites dans les forêts et l'agriculture (Hueth and Regev, 1974; Feder and Regev, 1975), et le cadre de modélisation bioéconomique a rapidement été appliqué à l'étude de la gestion optimale des espèces, à la fois "bonnes" et "mauvaises", par exemple le grand gibier et la sylviculture contre les parasites envahissants, en tirant parti de l'analyse des dynamiques des populations individuelles, sans beaucoup de processus spatiaux (Swanson, 1994; Skonhoft, 1999; Alexander, 2000; Horan et al., 2002). Dans les années 1990, un deuxième courant de modèles bioéconomiques a commencé à se concentrer sur la conservation optimale des espèces (au niveau de la communauté) afin de trouver des solutions pratiques de conservation de la biodiversité par le biais de la gestion de l'habitat, allant de la conception des réserves aux politiques agricoles promouvant la conservation (Costello and Polasky, 2004; Polasky et al., 2001, 2005; Wätzold et al., 2016; Mouysset et al., 2011). Les deux courants se sont développés et ont progressivement intégré les avancées de l'écologie, en particulier l'écologie paysagère (voir encadré 4) et ses processus spatiaux<sup>21</sup> et l'économie, avec les impacts de l'incertitude sur la prise de décision<sup>22</sup>, et la coordination d'agents ayant des intérêts concurrents et dans des contextes non coopératifs<sup>23</sup> (voir le chapitre

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<sup>21</sup>Cette littérature a été inaugurée par Huffaker et al. (1992); Brown and Roughgarden (1997); Sanchirico and Wilen (1999) qui ont d'abord étudié les interactions stratégiques et la dynamique de libre accès des métapopulations, avec une dépendance spatiale de la migration. Dans le même cadre, Sanchirico and Wilen (2005) étudie les politiques optimales de régulation d'une pêcherie de métapopulation en libre accès. Costello and Polasky (2008); Blackwood et al. (2010) sacrifient la dépendance à la densité pour la gestion optimale des biens et des maux à une grande échelle spatiale dans un espace discret. Brock and Xepapadeas (2010, 2020) développent des modèles utilisant le transport continu pour les espèces. Leur méthode permet de contourner les problèmes de dimensionnalité, mais nécessite la résolution d'équations aux dérivées partielles.

<sup>22</sup>La littérature sur la gestion des ressources naturelles a examiné comment le risque affecte la prise de décision avec des perspectives neutres vis-à-vis du risque (Reed, 1979; Costello and Polasky, 2008), le risque et les points de retournement écologiques (Costello et al., 2019) et l'aversion au risque (McGough et al., 2009; Kapaun and Quaas, 2013; Tahvonen et al., 2018). L'analyse de l'effet complet des différentes attitudes à l'égard du risque et du lissage de la consommation est une entreprise récente. En démêlant l'effet du risque et des préférences temporelles, Quaas et al. (2019); Augeraud-Véron et al. (2019) caractérisent la valeur d'assurance du capital naturel. Berry et al. (2019) analyse les effets d'assurance et de protection liés aux ressources naturelles et un risque écologique endogène. Récemment, Kelsall et al. (2023) ont caractérisé l'effet des préférences à l'égard du risque et de la variabilité intertemporelle du revenu sur l'extraction des ressources.

<sup>23</sup>Dans le sillage de la contribution séminale de Levhari and Mirman (1980) sur la guerre des poissons, de nombreuses contributions ont étudié la gestion des ressources dans des contextes non coopératifs, tels que Janmaat (2005); Kaffine and Costello (2010); Costello et al. (2015, 2017). D'autres courants de la littérature ont étudié la gestion des ressources dans des contextes d'intérêts contrastés, tels que les agents de conservation et des communautés agro-pastorales, Skonhoft (1998); ?

?? pour une revue approfondie de la littérature). Dans l'ensemble, les modèles bioéconomiques ont été utilisés à des fins diverses, couvrant toutes les utilisations mises en évidence par Varenne (2014) . Bien qu'ils aient progressivement intégré des dimensions et des complexités supplémentaires, ils restent confrontés à des défis pour traiter les moteurs du déclin de la biodiversité (Drechsler, 2020).

### Box 3 - Un bref aperçu de la modélisation écologique appliquée à la biodiversité

L'écologie est une branche de la biologie qui étudie les relations entre les organismes vivants et leur environnement.

Remontant à l'histoire naturelle de Humboldt (XVIII<sup>e</sup> siècle) et à l'entreprise de recensement du monde vivant, l'écologie a pris un tournant avec les travaux de Darwin sur l'évolution des espèces par la sélection naturelle (*On the Origin of Species*, 1859) pour devenir l'écologie évolutionne.

Au cours du XX<sup>e</sup> siècle, l'écologie s'est concentrée sur les fluctuations des populations d'espèces données et a commencé à utiliser des modèles mathématiques de la dynamique des populations (par exemple, la croissance logistique, (Verhulst, 1826), liant population totale, taux de croissance, et capacité de charge de l'écosystème) et des interactions entre les populations, comme les dynamiques proie-prédateurs (avec les travaux de Alfred J. Lotka (1925) et Volterra (1926)).

Au milieu du XX<sup>e</sup> siècle, l'écologie des communautés, issue d'études antérieures en histoire naturelle, a étudié la manière dont les communautés évoluent dans le temps après des perturbations, avec les travaux pionniers de MacArthur and Wilson (1967) qui étudient les schémas de richesse des espèces en fonction de caractéristiques géographiques plus larges et les modèles de métapopulations qui étudient les schémas spatiaux d'abondance des espèces (Levins, 1969; Roughgarden, 1974).

À la fin du XX<sup>e</sup> siècle, l'écologie paysagère a reconnu le rôle des modèles spatiaux dans la dynamique écologique. L'arrangement spatial des parcelles d'habitat est devenu le point focal et les méthodes ont commencé à inclure les systèmes d'information géographique (SIG) et les modèles de population d'une ou de plusieurs espèces explicites sur le plan spatial (modèles de métapopulation et de métacommunauté), considérant progressivement le paysage comme un réseau interconnecté d'îlots (Hanski, 1998; Urban and Keitt, 2001), où des causes stochastiques (démographiques, environnementales, génétiques) et extrinsèques (perte d'habitat, persécution, compétition avec d'autres espèces) affectent des populations réparties dans l'espace (Hanski, 1998).

À peu près au même moment, l'écologie de la conservation (Soulé, 1986) s'est attaquée à la perte de biodiversité et s'est concentrée sur la prévention des extinctions et la préservation de la diversité des espèces. Des outils comme l'analyse de la viabilité des populations, les modèles de risques d'extinction et les modèles de distribution des espèces ont été développés à cet égard.

## **Les défis de la modélisation pour lutter contre la surexploitation, la perte et la fragmentation de l'habitat**

Les modèles bioéconomiques sont généralement dynamiques, ont progressivement inclus les effets de la stochasticité économique et environnementale<sup>24</sup>, mais ils sont confrontés à des défis généraux, tels que l'inclusion des approches participatives et des connaissances indigènes<sup>25</sup> dans leur formulation et leur résolution. En outre, comme la plupart des publications se sont concentrées sur la dynamique des populations pour des espèces uniques<sup>26</sup>, même dans les modèles spatiaux granulaires (Sanchirico and Wilen, 1999, 2005; Costello and Polasky, 2008; Brock and Xepapadeas, 2010; Sanchirico et al., 2010; Albers et al., 2010; Costello et al., 2017) (c'est-à-dire comportant des métapopulations ou modèles de transport de population en espace continu), la modélisation explicite des communautés à travers l'espace reste un défi, afin de caractériser pleinement l'évolution de la diversité avec les politiques. Se concentrer sur l'habitat peut aider à adopter une perspective communautaire et à surmonter les limites des données, en utilisant les relations entre l'aire des espaces d'habitat et la distribution des espèces (MacArthur and Wilson, 1967) bien que des difficultés subsistent pour agréger l'habitat de différentes espèces au sein d'un cadre uniifié d'analyse. Toutefois, l'utilisation d'approximations peut entraver la dynamique spécifique des communautés, et il convient d'utiliser, dans la mesure du possible, des données sur l'abondance et la richesse au niveau de la communauté.

Les modèles bioéconomiques doivent tenir compte de différents objectifs. D'une part, l'utilisation et la préservation optimales de la biodiversité doivent être étudiées, afin que nous puissions concevoir les politiques appropriées pour y parvenir. D'autre part, les modèles bioéconomiques peuvent être utilisés pour anticiper et évaluer les performances comparées de politiques, particulièrement lorsque la mise en œuvre immédiate des meilleures politiques est impossible et que seules des politiques de second choix sont disponibles. Par conséquent, divers modèles peuvent être utilisés pour différents objectifs, mais ils doivent intégrer des possibilités d'effectuer des analyses de second choix (Lipsey and Lancaster, 1956).

Des défis plus spécifiques se posent pour remédier à la perte et à la fragmentation des habitats, et à la surexploitation des espèces. Dans l'ensemble, l'intégration de l'espace dans la modélisation bioéconomique reste une voie de recherche fructueuse. Comme souligné précédemment, les rôle de l'hétérogénéité

<sup>24</sup>Drechsler (2020) a néanmoins souligné que la stochasticité restait une caractéristique atypique des modèles bioéconomiques

<sup>25</sup>"Ensembles dynamiques de connaissances, pratiques et croyances sociales et écologiques intégrées, holistiques, relatives à la relation des êtres vivants, y compris les personnes, entre eux et avec leur environnement", dans le cadre de l'IPBES - traduit par l'auteur

<sup>26</sup>Une exception notable est Brock and Xepapadeas (2002), qui modélise l'évolution de N espèces , bien que sans espace

spatiale et de la dispersion ont été progressivement inclus dans la boîte à outils bioéconomique. Toutefois, l'analyse de la détermination endogène de la connectivité et de la dispersion spatiale reste à accomplir<sup>27</sup>. Cela soulève d'importants problèmes techniques. Tout d'abord, lorsque l'espace est discrétilisé, le nombre de variables d'état augmente considérablement. Pour les processus qui dépendent des variables d'état, l'augmentation du nombre de variables d'état conduit à la fameuse "malédiction de la dimensionnalité" (Bellman, 1957), où la programmation dynamique échoue. Cela nécessite un ajustement technique pour les solutions globales<sup>28</sup> comme l'adaptation de l'espace de recherche (Brumm and Scheidegger, 2017), ou le recours à différentes méthodes de résolution telles que les réseaux neuronaux pour l'interpolation de la fonction de valeur (Friedl et al., 2023). Des pistes fructueuses apparaissent lorsque l'espace est décrit comme un continuum et que les processus de diffusion sont décrits à l'aide d'équations aux dérivées partielles (Brock and Xepapadeas, 2010, 2020), objets nonobstant mathématiquement complexes. Lorsque l'espace est discrétilisé, l'augmentation de la résolution spatiale d'un modèle se fait souvent au détriment d'autres dimensions, telles que la dimension temporelle ou la complexité des processus économiques et/ou biologiques<sup>29</sup>. L'optimisation des interactions spatiales pour maximiser le bien-être peut s'avérer difficile en raison de la présence de non-convexités. Comme le montre l'encadré 3, la connectivité - définie comme la relation entre les parcelles d'habitat et les chemins qui les relient - peut présenter un comportement non globalement convexe. En d'autres termes, la connectivité peut ne pas augmenter de manière linéaire ou régulière au fur et à mesure que des parcelles ou des chemins sont ajoutés. Par conséquent, la fonction objective régissant l'optimisation de la connectivité peut ne pas bien se comporter, en particulier en présence de contraintes non convexes. Cela peut entraîner des difficultés dans la recherche d'optima globaux, car les solutions locales peuvent ne pas garantir des résultats optimaux en termes de bien-être.

Troisièmement, les outils issus de l'écologie paysagère, tels que la théorie des graphes appliquée aux réseaux écologiques, constituent une caractéristique

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<sup>27</sup>Une exception notable est Brock and Xepapadeas (2010) qui endogénise la formation des réseaux écologiques en économie

<sup>28</sup>Selon Brumm and Scheidegger (2017), les « solutions globales » désignent les « solutions calculées en utilisant les conditions d'«équilibre en de nombreux points de l'espace d'état d'un modèle dynamique », par opposition aux "solutions locales" qui reposent sur "une approximation locale autour de l'état d'équilibre d'un modèle, telle qu'obtenue par des méthodes de perturbation » d'après Friedl et al. (2023), p. 1.

<sup>29</sup>Par exemple, Blackwood et al. (2010), ? développent des modèles spatiaux étendus avec une croissance linéaire (par ex. croissance constante par habitant), Costello and Polasky (2008) développer un modèle sans dépendance des stocks sur les modèles de migration, ou Epanchin-Niell and Wilen (2012) développent un modèle d'automate cellulaire pour la propagation des ravageurs dans un cadre de programmation en nombres entiers, modélisant la présence d'une espèce et non pas sa population et sa croissance

fructueuse mais peu caractéristique des modèles bioéconomiques (Drechsler, 2020)<sup>30</sup> pour gérer efficacement les grands problèmes d'optimisation spatiale .

Cette difficulté s'accroît lorsque l'on considère des contextes stratégiques et non coopératifs (Levin et al., 2013). En effet , avec une dynamique dépendant de l'état, il est notoirement difficile d'augmenter le nombre de joueurs. Sur les réseaux, la détermination des équilibres non coopératifs est difficile (Bramoullé et al., 2014), en particulier avec des réseaux endogènes et plus d'une variable de choix stratégique, par exemple l'utilisation des ressources et la connectivité (Chen et al., 2018; Sadler and Golub, 2023). L'augmentation de l'hétérogénéité entre les types d'agents est également importante pour comprendre les moteurs de la connectivité et de la surexploitation (ou du contrôle). Il s'agit d'un défi, car un comportement non-symétrique peut conduire à des difficultés lors de la détermination de l'équilibre, même dans des contextes non spatiaux. Les sources d'hétérogénéité peuvent inclure la productivité écologique et les coûts et bénéfices économiques, au sein et entre des formes fonctionnelles (par exemple, coûts linéaires quadratiques contre coûts linéaires). Avec l'augmentation de l'hétérogénéité, la tractabilité analytique devient difficile, et la modélisation bioéconomique doit recourir à des méthodes numériques. Il est cependant essentiel que les modèles conservent une fonction heuristique (c'est-à-dire expliquer des phénomènes isolés) tout en augmentant leurs rôles prescriptif et prédictif.

Dans les interactions stratégiques de marché, telles que le monopole ou le duopole appliqués aux ressources renouvelables, les questions d'organisation industrielle ne sont pas encore pleinement résolus (Damania and Bulte, 2007). L'hétérogénéité économique (telle que des productivités de récolte ou des structures de coûts différentes) entre les acteurs stratégiques est importante pour déterminer l'évolution des ressources dans un contexte stratégique.

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<sup>30</sup>Une exception notable est ? qui considère un réseau de pêcheries connectées par le biais de mesures issues de la théorie des graphes afin de déterminer les zones protégées les plus rentables, avec une croissance linéaire du stock de poissons

## Questions de recherche

Dans cette thèse, je me concentre sur le rôle de 3 CNP, à savoir la création et le maintien de l'habitat<sup>31</sup>, la régulation des organismes nuisibles à l'homme<sup>32</sup>, et la fourniture par la biodiversité de matériaux et d'assistance<sup>33</sup>, sur terre et en mer.

Comme je l'ai exposé précédemment, les principaux facteurs qui menacent la biodiversité (à différentes échelles) et la fourniture de ces CNP sont la perte et la fragmentation de l'habitat, ainsi que la surexploitation (et le sous-contrôle) des espèces. Les politiques existantes n'ont pas réussi à enrayer le déclin de la biodiversité, et des recherches scientifiques supplémentaires peuvent aider à affiner la conception des politiques. La modélisation bioéconomique fournit un cadre utile pour intégrer l'écologie et l'économie afin d'orienter les politiques, mais elle est confrontée à plusieurs défis méthodologiques. Dès lors, dans le cadre de ma thèse, je m'interroge sur les questions suivantes :

1. Quels sont les effets des processus spatiaux endogènes sur les moteurs de la perte de biodiversité? Comment peut-on les gérer pour atténuer le déclin observé?
2. Quels sont les effets des comportements stratégiques sur les facteurs de perte de biodiversité?
3. Comment les modèles bioéconomiques peuvent-ils être affinés pour prendre en compte ces effets?

## Déroulé de la thèse

Pour répondre à ces questions, ma thèse comporte 4 chapitres , qui abordent ces questions de recherche en utilisant différents outils et questions de recherche spécifiques.

Dans le premier chapitre, je passe en revue la littérature sur les modèles bioéconomiques appliqués à la gestion des systèmes socio-écologiques terrestres, d'un point de vue méthodologique et narratif, afin d'acquérir une compréhension générale du domaine ainsi que des lacunes de la littérature qui restent à combler. Dans ([Jean and Mouysset, 2022](#)), nous avons mis en évidence deux paradigmes principaux structurant le domaine, sous la forme de réévaluations modernes du dé-

<sup>31</sup>"La formation et la production continue, par les écosystèmes, des conditions écologiques nécessaires ou favorables aux êtres vivants importants pour l'homme", ([Díaz et al., 2018](#)), Tableau S1

<sup>32</sup>"La régulation, par les écosystèmes ou les organismes, des ravageurs, des pathogènes, des prédateurs, des compétiteurs, parasites et organismes potentiellement nuisibles" ([Díaz et al., 2018](#)), Tableau S1

<sup>33</sup>"Production de matériaux dérivés d'organismes dans des écosystèmes cultivés ou sauvages et utilisation directe d'organismes vivants pour la décoration, le transport, l'entreprise et la main-d'œuvre", ([Díaz et al., 2018](#)), Tableau S1

bat conservationniste/préservationniste (Banzhaf, 2019) au début du 20e siècle. D'une part, un paradigme de "récolte raisonnée" étudie l'utilisation optimale (ou le contrôle) des ressources, évaluées de façon monétaire et les politiques qui les mettent en œuvre, appliqués aux espèces menacées, aux espèces envahissantes et aux parasites, ainsi qu'à la sylviculture, et principalement le fruit d'études par des économistes. D'autre part, un paradigme plus récent, autour de la "conservation de la biodiversité", se concentre sur la manière la plus rentable de conserver une variété d'espèces, dans des paysages faiblement ou fortement gérés (par exemple, agricoles), qui adoptent une perspective plus interdisciplinaire. Ce chapitre a mis en évidence les défis méthodologiques associés à la modélisation bioéconomique et les lacunes en matière de connaissances, que j'ai utilisés pour développer le reste de ma thèse.

	Chapitre 2	Chapitre 3	Chapitre 4
Perte et fragmentation de l'habitat			
Surexploitation, sous contrôle			

Table 1: Distribution thématique des chapitres

	Chapitre 2	Chapitre 3	Chapitre 4
Prisme de décision	Planificateur social	Planificateur social, équilibre non-coopératif	Equilibre non-coopératif
Espace	Petite et grande échelle	Petite échelle	Absent
Horizon temporel	5 pas, 10 pas	Infini	Infini
Type d'hétérogénéité	Structurelle du réseau	Ecologique et économique	Economique
Méthode de résolution	Heuristiques spatiales	Analytique et numérique	Analytique et numérique
Applications	Simulations	Simulations	Empirique
Niveau de biodiversité	Communauté	Population	Population
Tradition écologique	Landscape	Population et paysagère	Population
Unité de mesure	Parcelle	Individus (abondance)	Individus (abondance)

Table 2: Caractéristiques des modèles employés dans les chapitres de la thèse

Dans les chapitres 2 et 3, je me concentre sur l'économie de la perte d'habitat et de la connectivité, dans les paysages terrestres, et j'intègre l'espace comme variable de décision dans les modèles bioéconomiques. Les variables de décision sont localisées dans l'espace (par exemple, la taille de la population, la quantité d'habitat, les coûts, etc.) et font l'objet d'une décision en relation avec leur environnement: leur localisation et leur connectivité sont au cœur du problème de décision . Dans les deux chapitres, la connectivité structure des phénomènes

différents, des objectifs parfois contradictoires et déclenche des mécanismes politiques différents.

Dans un deuxième chapitre, avec L. Mouysset, nous considérons la gestion de la connectivité des paysages. Nous étudions la gestion dynamique et spatiale optimale de la connectivité des paysages forestiers, lorsque l'habitat de la biodiversité et le risque et les dommages liés aux incendies de forêt dépendent tous deux de la connectivité. Dans notre modèle, les parcelles forestières adolescentes favorisent l'habitat de la biodiversité, mais lorsqu'elles se transforment en parcelles forestières matures, elles risquent d'être touchées par des incendies de forêt. Un planificateur social choisit la répartition spatiale des traitements des combustibles de manière dynamique, de sorte que les traitements dans chaque parcelle réinitialisent le stade de succession à juvénile, où le risque d'incendie de forêt et l'habitat de biodiversité sont absents : la réduction du risque d'incendie de forêt nuit à l'habitat de biodiversité. Le planificateur social cherche à minimiser la connectivité des parcelles présentant un risque d'incendie de forêt, tout en maintenant la connectivité de l'habitat de la biodiversité, sous une contrainte budgétaire. Nous adoptons une perspective d'écologie paysagère dans laquelle les parcelles forestières sont l'unité de mesure de la biodiversité (habitat fourni à une communauté) et du risque d'incendie. Dans notre analyse, les variables d'état spatiales sont discrètes, et la connectivité est une fonction non-convexe : la connectivité incrémentale d'une parcelle dépend du phénomène considéré (risque d'incendie de forêt ou habitat) ainsi que de son environnement. En outre, le problème d'optimisation spatiale est rendu plus complexe par des contraintes sur l'ensemble des parcelles traitables, car la connectivité de l'habitat est importante. Avec cet objectif complexe, nous pouvons adopter une perspective spatiale et contourner la malédiction de la dimensionnalité en limitant la dynamique de la végétation à trois stades de succession. Ce faisant, nous montrons que l'optimisation myope répétée est équivalente à l'optimisation dynamique sur un horizon de planification de 5 périodes. Nous décrivons la frontière des possibilités de production entre les deux objectifs, et en utilisant un cadre de théorie des graphes, nous caractérisons les règles d'allocation de traitement à petite échelle pour une application générale. Malheureusement, les règles d'allocation de traitement à petite échelle ne s'étendent pas à une dimension plus grande, ouvrant de large perspectives à des travaux futurs.

Dans le troisième chapitre, j'étudie la gestion des maux publics mobiles et distribués dans l'espace (Costello et al., 2017). Dans cette littérature, l'impact des schémas de dispersion sur la gestion optimale et non coopérative a été largement étudié. Cependant, les modèles existants considèrent généralement que les mouvements sont donnés ou dépendent des densités de population relatives

(Huffaker et al., 1992; Bhat et al., 1996; Sanchirico and Wilen, 1999), mais ne tiennent pas compte de la façon dont les décisions humaines affectent ces schémas de mouvement. En effet, le flux d'espèces d'une parcelle à l'autre peut être entravé par des obstacles, par exemple, d'un point de vue conceptuel, par des clotûres: les réseaux écologiques comportent une couche humaine, un processus de décision endogène, et ne sont pas exclusivement déterminés par les caractéristiques écologiques. D'une part, l'élévation des clôtures dissout la connectivité du paysage et résout les externalités spatiales. Ce faisant, elle favorise un contrôle efficace des nuisances, même dans des contextes non coopératifs. Cependant, en présence d'hétérogénéité spatiale (écologique ou économique), il peut être préférable d'exploiter ces différences comme des opportunités d'arbitrage, afin de maximiser le bien-être : les nuisibles peuvent être enfermés là où leur gestion est peu coûteuse, ou là où ils se reproduisent à un taux plus faible. Dans ce chapitre, je commence par caractériser la gestion spatiale optimale d'un mal public mobile du point de vue du planificateur social en présence d'hétérogénéités économiques et écologiques entre les parcelles. Ensuite, j'étudie l'équilibre décentralisé dans un cadre non coopératif, où les propriétaires terriens peuvent construire des clôtures et contrôler un parasite. Je montre que si les clôtures peuvent résoudre la tragédie des biens communs, l'équilibre décentralisé peut aboutir à une allocation sous-optimale en présence d'hétérogénéités écologiques et économiques, car les possibilités d'arbitrage spatial ne sont pas épuisées.

Dans le quatrième chapitre, co-dirigé avec J.Lawson, nous étudions le sort de *Totoaba macdonaldi*, une espèce de poisson endémique dans le Golfe de Californie au Mexique. La pêche et le commerce de *Totoaba* ont été interdits par la Convention sur le commerce international des espèces de faune et de flore sauvages menacées d'extinction (CITES) pendant 50 ans, ce qui a permis de reconstituer le stock de la population. Néanmoins, les données indiquent une résurgence significative du braconnage. Le *Totoaba macdonaldi* est très prisé pour sa vessie natatoire sur les marchés chinois, et son commerce est contrôlé par un groupe criminel organisé. Tirant parti d'une multitude de nouvelles données, nous relançons le cadre élaboré par Damania and Bulte (2007). Nous étudions si le contrôle du totoaba par un monopole vertical peut être bénéfique pour l'espèce. Nous constatons que les résultats sont sensibles à des incertitudes relatives aux données, sur les coûts et paramètres écologiques, et nous analysons si la substitution par l'aquaculture peut constituer une alternative viable. Contrairement au cadre original, nous montrons que la concurrence n'entraîne pas nécessairement l'effondrement des stocks et qu'elle pourrait réduire de manière significative (-29%) le braconnage et les profits illégaux (-195 millions de dollars US).

## Résumé des publications et participations à des conférences

**Chapitre 1 : Bioeconomic Models for Terrestrial Social Ecological System Management : a Review**, S.Jean et L. Mouysset, *International Review of Environmental and Resource Economics*, DOI : 10.1561/101.00000131

Le code et les données sont publiquement accessibles

Présentations :

- European Association of Environmental and Resource Economists (EAERE) Annual Conference, Rimini, 2022
- Journées Doctorales ABIES - Prix du meilleur poster scientifique, 2022

**Chapter 2 : The Wildfire-Habitat Connectivity Dilemma: a Graph Theoretical Approach to Landscape Management**, S.Jean et L. Mouysset, *Working Paper*

Le code et les données sont publiquement accessibles

Présentations :

- Séminaire BINGO, CIRED, 2023
- Interdisciplinary PhD Workshop in Sustainable Development, Columbia University, 2023

**Chapter 3 : Fences - the Economics of Movement in Mobile Public Bads**, S. Jean, *Working Paper*

Les codes de réPLICATION sont publiquement accessibles

Presentations :

- PhD Seminar of the French Association of Environmental and Resource Economists, Université Savoie Mont-Blanc, 2024
- Parisian PhD Seminar in Environmental Economics, Nogent sur Marne, 2024
- Séminaire interne du CIRED, 2024
- Séminaire inter de l'équipe Biodiversity Economics, iDiv, Leipzig, 2024

**Chapter 4: Little downside and substantial gains result from farming of To-toaba Macdonaldi**, J. Lawson, S.Jean (co-premier auteurs), A. Steinkruger, M. Castellanos-Rico, G.M. Goto, M.A. Cisneros-Mata, E. Aceves Bueno, M.M. Warham, A.M. Sachs and S.D. Gaines, en révisions à *NPJ Ocean Sustainability*

Le code et les données sont publiquement accessibles.

Presentations:

- BIOECON Network Annual Conference, Université de Santiago de Compostela, 2023
- Trade and the Environment, Paris Saclay Applied Economics, 2023
- European Association of Environmental and Resource Economists Annual Conference, Université de Leuven, 2024

# Introduction

Humanity is amidst a critical ecological era, whereby the ecological thresholds of the earth system have been crossed. The notion of "planetary boundaries" (Rockström et al., 2009; Steffen et al., 2015) illustrates how the anthroposphere, the planetary-scale effects of human activities, have become an additional functional component and are capable of changing the Earth system (Richardson et al., 2023) alongside the geosphere (energy flow and nonliving materials in Earth and atmosphere) and biosphere (all living organisms/ecosystems). The "planetary boundaries" framework identifies the limits to the impact of the anthroposphere on the Earth system that can safeguard Earth's interglacial state - the only one where civilization is known - by identifying a "safe operating space". Among these nine boundaries, Richardson et al. (2023) estimate that 6 have been crossed, threatening the stability and resilience of the Earth system.

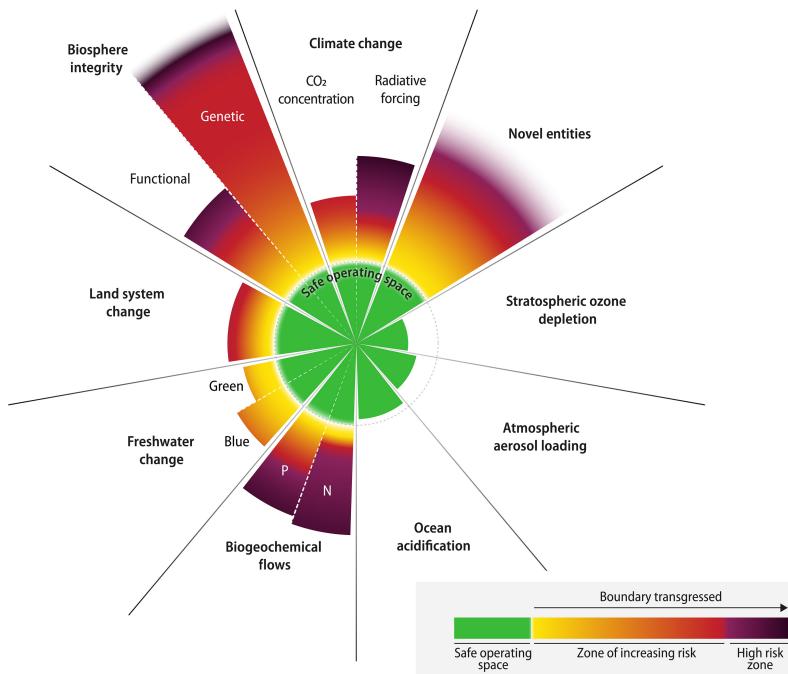


Figure 1: Current status of control variables for all nine planetary boundaries, from Richardson et al. (2023)

Among these planetary limits, the integrity of the biosphere has gradually become of particular interest, along with its interaction with other limits, such as climate change, or novel entities (e.g. synthetic organic pollutants, radioactive

materials, microplastic pollution...). Created in 2012, the Interdisciplinary Panel on Biodiversity and Ecosystem Services (IPBES) has been raising the alarm on the state of "Nature" globally. Its chair, Sir Robert Watson, put it clearly<sup>34</sup>:

*The overwhelming evidence of the IPBES (2019) Global Assessment from a wide range of different fields of knowledge, presents an ominous picture [...]. The health of ecosystems on which we and other species depend is deteriorating more rapidly than ever. We are eroding the foundations of our economies, livelihoods, food security, health and quality of life worldwide*

"Nature" is a central concept in the IPBES framework (IPBES, 2019):

*Nature (also defined as living nature) [is] the nonhuman world, including coproduced features, with particular emphasis on living organisms, their diversity, their interactions among themselves, and with their abiotic environment. Within the framing of natural sciences, nature includes e.g. all dimensions of biodiversity, species, genotypes, populations, ecosystems, the biosphere, ecosystem functioning, communities, biomes, Earth life support's systems and their associated ecological, evolutionary, biogeochemical processes and biocultural diversity. Within the framework of economics, it includes categories such as biotic natural resources, natural capital, and natural assets. Within a wider context of social sciences and humanities and interdisciplinary environmental sciences, it is referred to with categories such as natural heritage, living environment, or the nonhuman. Within the context of other knowledge systems, it includes categories such as Mother Earth [...], Pachamama [...]*

IPBES (2019), p.14, see also Díaz et al. (2015)

Nature, as defined in this approach, is a very large and complex object. It is defined across ontological and epistemic differences (living and non-living e.g. matter), different types of interactions, at various scales (genotypes v. ecosystems), at different types of processes (biological v. ecological), and across different fields of inquiry (natural sciences v. social sciences). In this dissertation, I study more specifically "biodiversity", which focuses on the variability among living organisms. While it is itself an ambiguous concept, biodiversity tends to put the focus on living organisms, in relation to their material, biotic and abiotic environment (as opposed to the study of the non-living environment) and on its critical role among other components of the Earth system.

The IPBES (2019) report documents the drastic changes the biosphere is going through and considers these changes through an anthropocentric lense, i.e. mediating the aforementioned changes through the multiple and diverse contributions

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<sup>34</sup>See the [press release address](#) of the 2019 report

that Nature and biodiversity bring to people. It stresses how their disruption impacts human lives and highlights the role of anthropogenic (i.e. of human origin) drivers of the disruption of nature and biodiversity.

This report sets different objectives to scientific research. The first objective is to explain the feedback mechanisms : how do human livelihoods impact biodiversity? In response, how does biodiversity impact human livelihoods? This objective involves understanding the causes and measuring the direct and indirect anthropogenic drivers of change in nature and biodiversity on the one hand, and on the other hand understanding the channels and scales through which nature and biodiversity contribute to human livelihoods, as well as measuring these contributions. Hence, studying the demise of nature and the potential to remedy it calls for an integrated perspective, that joins natural sciences to social sciences, through frameworks such as social-ecological systems ([Ostrom, 2009](#)) or environmental and ecological economics ([Daly, 2007](#)).

The second objective is to provide a framework to assess the desirability, the feasibility and means of implementation of collective pathways that would remedy the crisis nature is facing. In a way, it involves designing and implementing policy pathways towards sustainable futures, e.g. finding definite courses or methods of action selected from alternatives, at the individual, collective or governmental levels, to achieve future states of the world which remain in a safe operating space regarding planetary bounds ([Rockström et al., 2009; Steffen et al., 2015](#)).

In this dissertation, I take on these two objectives using a framework stemming from economics and ecology. A first version of the research questions this thesis aims at solving is:

1. What are the feedback relationships between biodiversity and anthropogenic drivers of its decline?
2. What underlying mechanisms must policy pathways tackle to remedy this demise?
3. How can integrated economic and ecological approaches be used and refined to analyze inform and design policies?

In order to refine these questions, I first define the concept of biodiversity, through its natural and social sciences appraisals, and highlight ongoing trends in its demise.

## Emergence and definition of biodiversity as an ecological concept

Biodiversity emerged as a concept in the 1980s, along with the emergence of "conservation biology", a branch of biology concerned with the protection of "biological diversity" (Soulé, 1985), as a response to an acceleration in the loss of species. The moral stance of conservation biology is that species should be protected for their own sake (Soulé, 1986), they have intrinsic value. The concept of biodiversity is therefore embedded in an ethical judgement and a call for action. In the wake of the 1992 Rio United Conference on Environment and Development, the [Convention on Biological Diversity](#) emerged as an international treaty to safeguard biodiversity. In doing so, it provided an internationally agreed upon definition:

*"Biological diversity" means the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems.*

[Article 2 of the Convention on Biological Diversity](#)

This definition highlights a key differentiating feature from other parts of nature, i.e. the living nature of the objects of study. Compared to abiotic factors, biological diversity is characterized by intrinsic growth, reproduction and metabolism (at the individual and population levels), and evolution (at the genetic, and species level). Additionally, these rates of change through time are commensurable with human experience, and most processes (i.e. reproduction, population collapse or recovery, genetic evolution) can be observed within a human lifetime as opposed to the geological temporal scale.

As highlighted by [Dyke and Lamb \(2008\)](#) and [Mouysset \(2023\)](#), the definition of biodiversity is difficult, as it recovers ethical, conceptual and measurement dimensions. Biodiversity can be viewed as "an intrinsic, value-laden quality of natural systems that should be preserved for its own sake" ([Dyke and Lamb, 2008](#); [Mouysset, 2023](#)), but it also refers to measurable features. This definition implies different scales from a hierarchical perspective, at the genetic level, at the species, the community, and the ecosystem levels (defined as the interaction of communities and their abiotic environment). These levels imply different forms of measurement, including the distribution of genes, species abundance (i.e. the number of individuals in a population, at a given time and location), species richness (i.e. the number of different species, at a given time and location) within communities, among communities, and across larger scales (i.e. alpha, beta and gamma diversities.), as well as variations in the abiotic factors that form ecosystems, such as temperature, humidity, water quality, soil quality etc. It also comprises different types of diversity : structural diversity (for example, the layers of canopy in

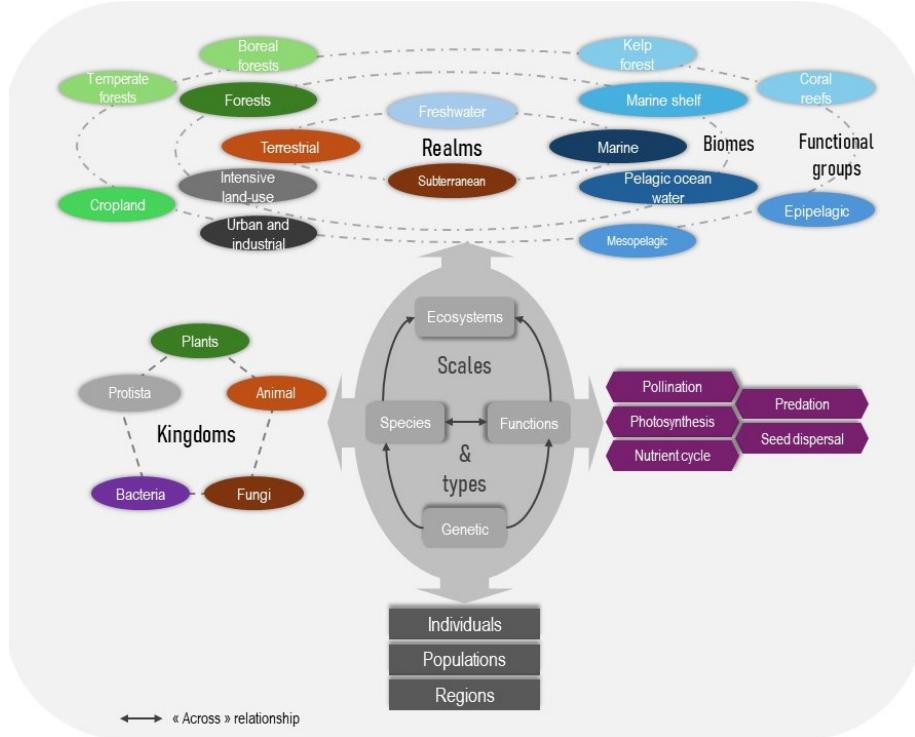


Figure 2: Biodiversity : a multiform concept across scales and types

forests, the sex-ratio in animal populations), compositional diversity (the variety and abundance of species within a community), and functional diversity (variety of environmental processes performed by living organisms in a given area i.e. carbon sequestration, nutrient cycling or seed dispersal, see [Loreau et al. \(2002\)](#))

[Mouysset \(2023\)](#) highlights the difficulty of articulating the definition with common levels in scientific analysis i.e. genetic, taxonomic, and ecosystem, as biodiversity level can fall in between: "populations may be considered from a genetic and taxonomic perspective, or communities that fall between the taxonomic and ecosystem levels". Additionally, as structural and compositional diversity can be seen as the source of functional diversity, the different classes of diversity may be difficult to work with given their colinearity.

The multiple dimensions of biodiversity highlight several of its critical features. First, it is impossible to measure biodiversity with a single indicator. The study of biodiversity requires multiple indicators to integrally assess the evolution of biodiversity, across scales and types of diversity. The emergence of the concept responds to a desire to protect biodiversity for its own, but also humanity's sake.

## Nature's Contributions to People: rationales for biodiversity conservation

Originally descriptive, ecosystem functions were increasingly viewed from a human perspective starting in the 1970s (Hueting, 1969; Schumacher, 1973), evolving into the concept of ecosystem services (Ehrlich, 1981) to illustrate biodiversity loss consequences (Gómez-Baggethun et al., 2010). This marked a shift from intrinsic to anthropocentric (i.e. given by humans) value (Mouysset, 2023), recognizing biodiversity's instrumental and relational values—serving human ends and fostering meaningful relationships. Gradually, biodiversity had to be protected for its role in sustaining human life.

The concept gained traction in academic research, and as Costanza et al. (1997) quantified the value of natural capital and ecosystem services, at a staggering 33 trillion \$USD, amounting to approximately 30% of the 2020 World GDP, the concept reached the policy arena. In 2005, the Millennium Ecosystem Assessment (Hassan et al., 2005) placed ecosystem services at the center of the policy agenda : it emphasized an anthropocentric value of ecosystem services, but established a dependence of human societies on ecosystem services, and further, on the functioning of ecosystem. In this respect, the Millennium Ecosystem Assessment Hassan et al. (2005) was a landmark in safeguarding biodiversity through a *strong sustainability* paradigm (see box 1), and triggered the operationalization of the concept into policy at a large scale (which I will develop later on). The ecosystem services framework was divided into 4 categories, relating to the specific type of services contributing to "human wellbeing" : supporting services (i.e. services allowing for other ecosystem services to be present, including nutrient cycling and primary production) and regulating services ("benefits obtained from the regulation of ecosystem processes" e.g pollination, waste decomposition etc); cultural services ("the nonmaterial benefits people obtain from ecosystems through spiritual enrichment, cognitive development") and provisioning services ("all the products obtained from ecosystems", Hassan et al. (2005), p.54)

Recently, the IPBES platform moved onto a new conceptual framework highlighting Nature Contributions to People (NCP) (Díaz et al., 2015), defined as "all the contributions, positive and negative, of living nature [...] to people's quality of life (Díaz et al., 2018)". This framework underpins 3 types of contributions to people: material contributions to people (flows from nature to people typically consumed to "operate a society or enterprise" (IPBES, p.16), non material contributions (eg. nature's effects on "subjective and psychological aspects underpinning peoples quality of life) and regulating contributions (i.e. "functional and structural aspects of organisms and ecosystems that modify the environmental conditions experienced by people and/or regulate the generation of material

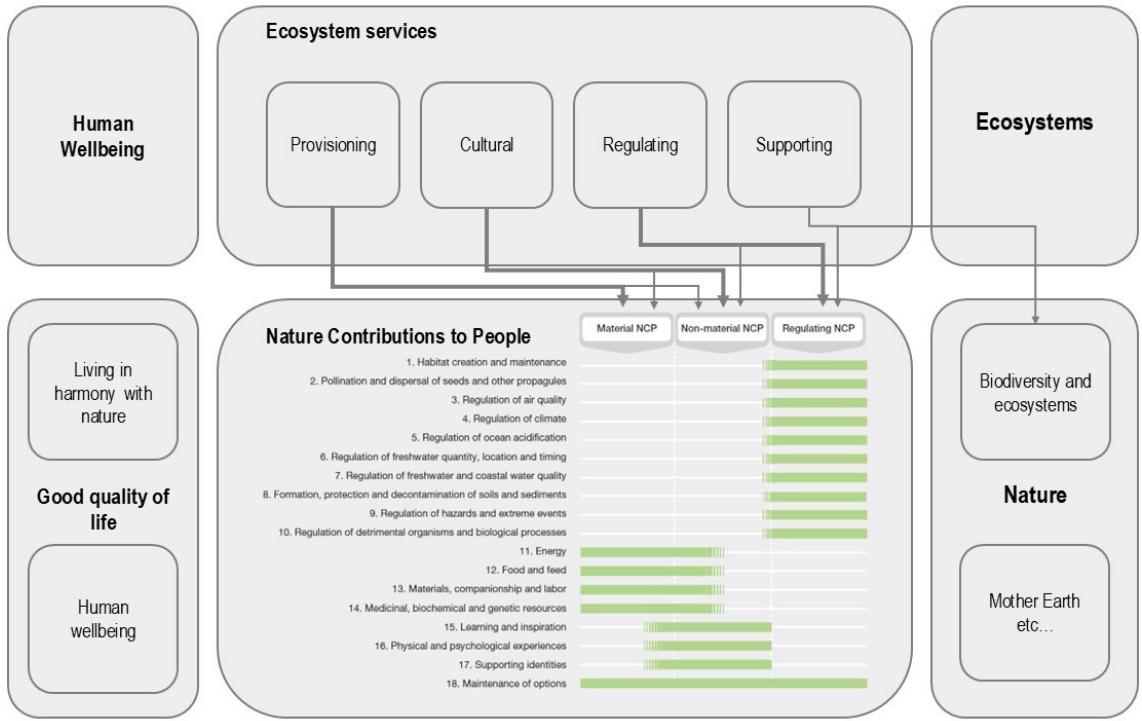


Figure 3: Description of the 18 Nature Contribution to People and the connection between the NCP framework (IPBES, 2019) and the Ecosystem Services Framework (Millennium Ecosystem Assessment, 2005)

Adapted from Diaz et al. (2018) and IPBES (2019)

and non material contributions"). This framework highlights how Nature Contributions to People can be positive or negative, and depend on the spatial and temporal definition of the contribution, as a given entity can be at the same time the source of positive and negative contributions: for example, forests foster habitat, but also risk endangering people in the event of wildfires. Additionally, it provides a more encompassing view than ecosystem services, as it encompasses perspectives ranging from biodiversity as natural capital employed in an ecological production function (see Polasky and Segerson (2009) for a review), as well as perspectives where biodiversity has agency and is linked by reciprocal care obligations to humans (Descola, 2013).

A multifaceted correspondence between the different components and dimensions of biodiversity and its contributions to people underpin human livelihood. The global decline of biodiversity threatens NCPs.

### Box 1 - Weak v. Strong Sustainability

In 1987, the release of the Brundtland Report ([WCED, 1987](#)) provided a broad definition of sustainable development:

*In essence, sustainable development is a process of change in which the exploitation of resources, the direction of investments, the orientation of technological development; and institutional change are all in harmony and enhance both current and future potential to meet human needs and aspirations*

[WCED \(1987\)](#), p.43

Implementing sustainable development remained an open question. In economics, a "weak sustainability perspective", pioneered by works of [Hartwick \(1977\)](#) and [Solow \(1986\)](#) on exhaustible resources, suggested that "maintaining a non-declining capital stock, which allegedly could be put into practice by investing in manufactured capital all the rents derived from the exploitation of non-renewable natural resources" ([Gómez-Baggethun et al., 2010](#)) was sufficient to maintain consumption through time. In this approach, natural capital could be integrally substituted by human made capital. On the other hand, the "strong sustainability" approach advocates for a complementarity, rather than substitutability, of natural resources ([Costanza and Daly, 1992](#)), acknowledging the dependence of humans on ecosystems.

## Decline in biodiversity : trends and drivers

Biodiversity metrics are declining across all the scales of analysis. The structural conditions of ecosystems, the compositions of ecological communities and populations of species have experienced dramatic changes.

The share of unchanged, protected wildlife habitat has plummeted on both land and sea ([Watson et al., 2016](#); [Jones et al., 2018](#)) to 23% and 12% of space, respectively. At the community level, the share of originally present biodiversity falls below 90% across all biomes, ([Hill et al., 2018](#)) and local communities are becoming more and more similar ([McKinney and Lockwood, 1999](#)), driven by the increased extent of animal and plant non-native invasive species, rising by 13% per decade ([Seebens et al., 2017](#)). At the species level, to date, global species richness is threatened by a mass extinction, as the global rate of species extinction is at least ten times higher than the average rate over the past 10 million years and is accelerating ([Barnosky et al., 2011](#); [Ceballos et al., 2015](#)). On average, 25% of species are currently threatened with global extinction across a wide range of plant and animal species, on land and at sea ([International Union for the Conservation of Nature \(IUCN\), 2018](#)).

vation of Nature - IUCN, 2024). Using habitat based methods<sup>35</sup>, Hoskins et al. (2020) find that hundreds of thousands of plant and animal species are threatened, and will repay the *extinction debt* caused by anthropogenic changes to their habitats : only 92.1% of terrestrial vertebrate species, 91.6% of terrestiral invertebrates and 90.7% of terrestrial plants have enough habitat to persist. These results suggest that around half a million terrestrial animal and plant species - including over 3000 vertebrates and over 40,000 plants - *dead species walking*, doomed to become extinct, unless their habitats improve in time to prevent it (IPBES, 2019).

Drivers of biodiversity decline are of anthropogenic origin. They can be classified between *direct* drivers, i.e. that directly flow from human actions, such as land use change, anthropogenic climate change, overexploitation, and *indirect* drivers, that can be viewed as the root cause for direct drivers, such as , changes in the value systems that underpin nature uses (IPBES (2019) p.55), demography (urbanization and migration), technology, economy (sectoral transitions, trade expansion) and governance (including right systems for access to resources).

A synthesis of natural sciences performed by IPBES (2019) outlines the roles of principal drivers at the global scale and across realms (see figure 4). It shows that land and sea use, referring to the loss, fragmentation<sup>36</sup> and degradation of wildlife habitat are responsible for 30% of the impacts on biodiversity. The direct exploitation of wildlife, wild plants and trees represents 23% of impacts. Climate change, through shifts in biogeographic conditions and changes in habitat, impacts on species traits and genetic evolution represents 14%, and pollution represents 14% of impacts. Finally invasive alien species represent 11%. These drivers

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<sup>35</sup>The IUCN Redlist uses detailed accounts for species, in a bottom-up approach, to analyze the extinction risk of species. A top-down approach, relying on the evolution of available habitat and the species-area relationship, uses changes in land use to forecast the extinction of species in a more aggregate manner (Diamond, 1972)

<sup>36</sup>Undoubtedly, habitat loss is the main driver of terrestrial biodiversity decline. The effects of fragmentation on biodiversity are highly debated. From a theoretical perspective, models have been developed to study the evolution of populations and communities through space and time, i.e. metapopulation and metacommunity models. Theoretical insights highlight that habitat fragmentation increase the extinction risk, and lower colonization probability, resulting in lower survival and diversity (Adler and Nuernberger, 1994; Hill and Caswell, 1999; Thompson et al., 2017). At the community scale, increases in diversity among communities (i.e. beta diversity) can emerge from different species resource requirements and the larger spatial extent, hence encompassing more environmental heterogeneity, that results from fragmentation (Lasky and Keitt, 2013; Chisholm et al., 2018). However, these effects dampen as habitat loss decreases. At the empirical level, the effect of fragmentation is highly debated. According to Fahrig (2017), there is no empirical evidence that a group of small habitat patches generally has lower ecological value than large patches of the same total area. Evidence is however found to show that fragmentation does not reduce habitat connectivity, as functional connectivity is improved (i.e. species are in contact with more different resource patches, thus improving the overall functioning of ecosystems). The debate between Fletcher et al. (2018) and Fahrig et al. (2019) surrounds critics based on the ability of statistical models to encompass the effect of fragmentation when habitat loss is present (Ruffell et al., 2016). Moreover, it reflects the difficulty of landscape ecology, as different mechanisms across scales i.e. patch, landscape and study region, and measures, such as patch size, patch isolation (i.e. distance across patches) and distance to patch edge (i.e. distance to edge within the patch) interact with possible non-linear interactions.

have differentiated impacts across ecosystems and biomes (IPBES, 2019).

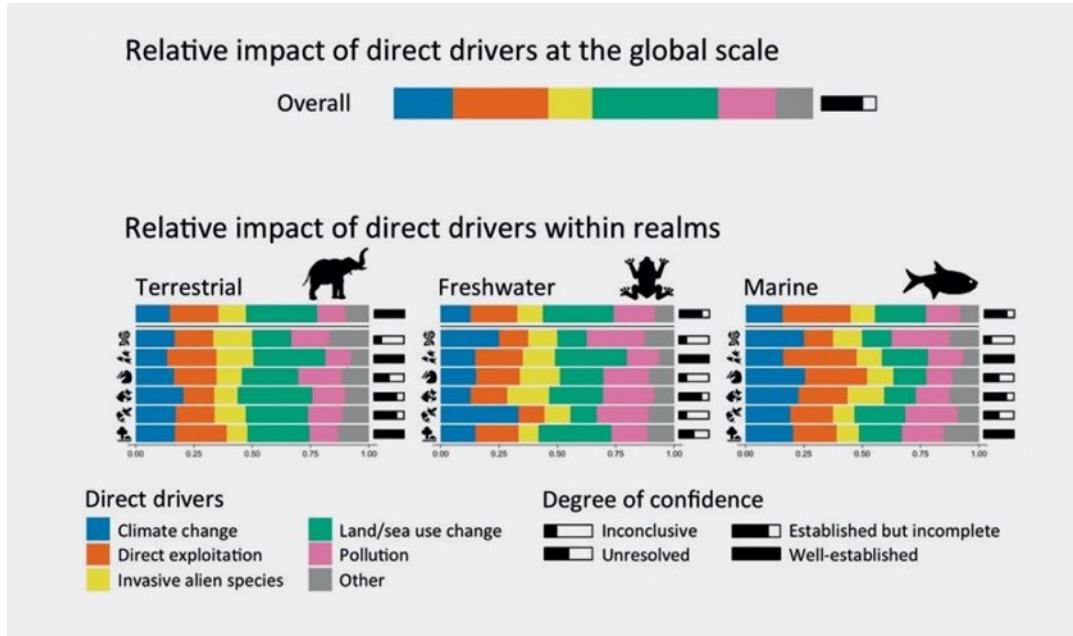


Figure 4: Aggregate and realms specific impacts of anthropogenic direct drivers of biodiversity decline adapted from IPBES (2019)

On land, land use change is the most important driver (30.5%), driven by deforestation and agriculture, and direct exploitation follows next (21%). Tropical and subtropical dry and humid forest host the greatest biological diversity. For example, they host the 10 hotspots with the greatest total number of vertebrates (Mittermeier et al., 2011). In such forests, habitat loss and degradation are the main drivers of reductions in species abundance and richness (Newbold et al., 2014). Legal and illegal selective logging destroy habitat (Hoare and Uehara, 2022; Bousfield et al., 2023) and are combined with hunting and poaching of wildlife (Gallego-Zamorano et al., 2020), generating between 60 and 180 billions \$ USD of revenue (GFI, 2017)<sup>37</sup>.

For marine species, overexploitation is the main driver (29%) (IPBES, 2019). With 90 million tons of capture (and 141 billion \$ USD) in 2020 (FAO, 2022), fisheries stock within biologically sustainable levels have decreased to 64.6% in 2019, from 90% in 1974<sup>38</sup>, driven by overfishing in the Southeast Pacific and the Mediterranean and Black seas. Nonetheless, illegal, unreported and unregulated (IUU) fishing is a threat to fisheries. Estimates from 15 years ago (Agnew et al., 2009) estimated it represented between 11 and 26 million tonnes of fish with a value of 10 to 23 billion \$ USD.

Additionally, anthropogenic climate change drives ecosystem disruptions on

<sup>37</sup>Illegal wildlife trade represents between 5 and 23 billion \$USD, while illegal logging represents 52 to 157 billion \$USD

<sup>38</sup>In this calculation, all fishery stocks are equally counted, irrespective of their abundance or catch

land (Burrell et al., 2020; Conradi et al., 2024) and at sea (Gomes et al., 2024), through changes in various channels including ecological suitability and food-web disturbances. On land, for example, mediterranean forests, woodlands and scrubs, covering 4 million km<sup>2</sup>, are areas of exceptionally high diversity too (Mooney et al., 2001; Blondel et al., 2010), threatened with urban expansion and increased wildfire risk. Wildfire frequency and severity are expected to increase with global warming (Dupuy et al., 2019), causing important direct and indirect costs to society including destruction of infrastructure and perturbations to economic activity (Wang et al., 2021), smoke related health conditions (Burke et al., 2023; Heft-Neal et al., 2023), disrupting structural features of ecosystems (Ayars et al., 2023) and threatening biological diversity (Wintle et al., 2020).

## Economic challenges of anthropogenic drivers of biodiversity decline

Habitat loss and overexploitation present both common and differentiated challenges. A common identifiable cause is the large opportunity cost of preserving a species habitat, or existence, in the presence of other economic alternatives for land and time, as well as financial constraints. Additionally, habitat loss and overexploitation share a temporal dynamic aspect, where immediate actions have durable consequences, possibly irreversible.

Habitat loss and fragmentation in terrestrial ecosystems present specific challenges. Forests, for example, serve multiple uses (or NCPs) to various agents: loggers profit from timber, settlers clear land for agriculture, hikers seek pristine landscapes, and conservationists aim to restore natural cycles. Forests also hold spiritual and cultural value, creating conflicts among these uses. For instance, deforestation and urbanization destroys both habitat and sacred land, but create measured economic value (Giglio et al., 2024) while wildfire prevention can damage wildlife habitat (Bradshaw et al., 2018). Species can also have mixed impacts; deer, for example, are valued at low densities but cause damage at higher densities (Putman et al., 2011). A second key feature to halt habitat fragmentation is considering the integral set of interdependencies, ecological spillovers and economic externalities that underlie the spatial dimension. The configuration of space, and species movement is at least partly the result of an economic decision. Maintaining habitat connectivity involves identifying patches and paths to be conserved or restored that contribute most to it, in the form of corridors, ecoducts or stepping stones (Turner, 2005; Turner and Gardner, 2015). The value of patches and paths for connectivity is intrinsically linked to their surrounding : at the same geographic location, a patch has differential value for biodiversity habitat if it is connected to others, or if it is isolated (see box 2). When paths are be-

yond human control, patches have different importance based on their location, and when the location of patches is fixed, the extent of paths and their location is paramount. Third, as multiple actions and uses structure connected elements of ecosystems (i.e. different tracts of land, or different biodiversity scales), they trigger spatial spillovers i.e. consequences that go beyond their *in situ* effects. When these spillovers are not taken into account by the agents that generate them, they can be called "dynamic spatial externalities" (Sanchirico and Wilen, 1999; Costello and Polasky, 2008; Costello et al., 2017). As halting habitat loss and fragmentation involves conserving tracts of land, neighboring parties may very well benefit (or suffer) from more wildlife and ecosystem (dis-)services on their property, through time. As agents respond to each other's action profiles, they behave strategically, both in space and time. These externalities can trigger specific problems of "race to the bottom" (Costello et al., 2017) : when neighboring parties of a decision maker that undertakes conservation, or risk reduction, fail to reciprocate as they benefit from spillovers, a vicious circle of least action is triggered. Conversely, when ecological spillovers are positive, this may lead everybody to use a resource at unsustainable levels, even in the presence of well defined rights, absent other mechanisms (Janmaat, 2005; Kaffine and Costello, 2010). Hence, habitat fragmentation and overexploitation are interrelated through spatial connectivity. Fourth, improving habitat loss and fragmentation involves coordinating numerous actors towards increasing the area and connectivity of habitat, while taking into account the associated costs and benefits, and different interests. In some cases, the financial constraints, the magnitude of costs associated with increased habitat connectivity and the difficulty of coordination warrant a public policy where a central planner undertakes the action (Mouysset et al., 2012). On the other hand, mechanisms to decentralize efficient spatial planning exist and can be efficient under limited costs of cooperation (Costello et al., 2017; Bareille et al., 2023).

Halting overexploitation requires understanding and addressing its motives. Overexploitation (or under control, for pests), results from an imbalance between the appropriation and incumbance of Nature's contributions to people (both positive and negative) and the socially desirable level and allocation of these contributions, as well as the uncoordinated, strategic behavior of agents. The common nature of most natural resources (Gordon, 1954; Smith, 1969) has long been identified as one of key reason for their demise: numerous events have shown a "race to the bottom", where the absence of secure property rights hastened the over-harvest and decline of populations. It has long been the center of attention, and mechanisms relying on property rights assignment have been studied extensively (Libecap, 2009; Costello et al., 2015; Isaksen and Richter, 2019).

## Box 2 - Habitat Loss, Fragmentation and Connectivity

Habitat loss refers to the loss of areas featuring suitable environmental conditions for species survival and development. At a constant habitat area, fragmentation refers to increases in the number of patches and decrease in the mean size area of each patches, as in figure 5.

Landscape connectivity is defined in relation to fragmentation. It measures "the degree to which the landscape facilitates or impedes movement among resource patches" (Taylor et al., 1993). It recovers a *structural* dimension, which describes the physical arrangements across patch and a *functional* dimension, which emphasizes the ability and realization of movements of individuals through the landscape.

Aggregate connectivity measures take into account the role of differentiated patches and paths. In panel D of figure 5, the circled patches play an instrumental role in maintaining connectivity. Habitat patch 1 and 2 have the same number of connected patches. However, patch 1 is maintains the connection between the east and west habitat patches in the landscape, and is connected to highly connected patches. Removing habitat patches 1 and 2 would have larger consequences on habitat than removing other identical size patches. Similarly, removing the dotted path (bottom left of panel D) would isolate patch 3, while removing the dashed path would not leave patch 4 isolated. Hence, paths and patches have different impacts on connectivity, depending on the surrounding patches and paths.

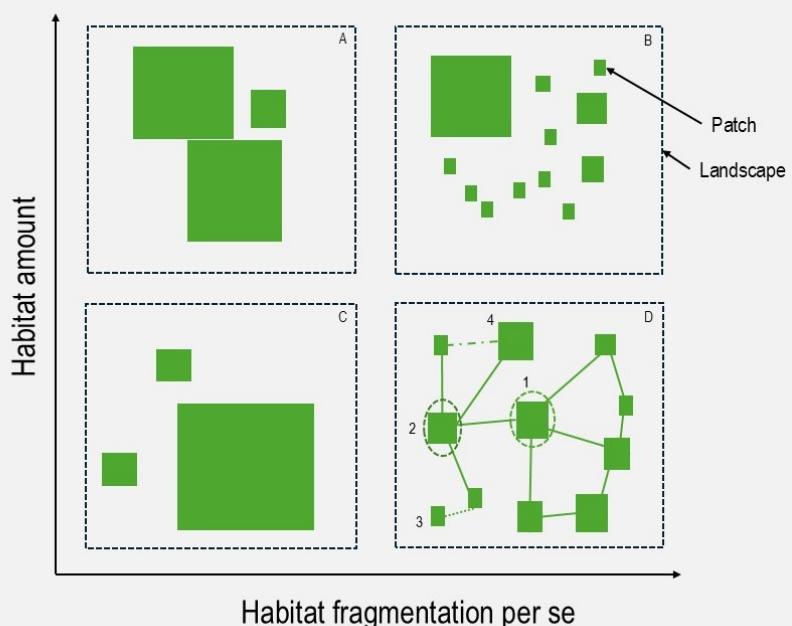


Figure 5: Illustration of the effects of habitat loss and fragmentation, adapted from Fahrig et al. (2019), and of connectivity

However, while property rights may be assigned, they can be notoriously hard to enforce in areas where regal functions are challenged: *de facto* rights are assigned and enforced. In this case, the common nature of the resource may not be the main concern: local market concentration forces may outweigh overexploitation forces, even in the presence of some form of open access ([Damania and Bulte, 2007](#)). Around the world, wildlife poaching and trade typically originates from organised crime groups, and is associated with different criminal activities ([Mozer and Prost, 2023](#)). Concentrated markets tend to emerge and characterize wildlife markets, as competition is hindered by violent organised crime groups. In this case, resource management is strategic and responds to market characteristics (demand structure, intermediary input price) and ecological characteristics (distribution of species, biological growth rate, carrying capacity<sup>39</sup> of the ecosystem)

At one extreme, locally monopolistic markets structure for wildlife products may emerge, especially in the case of endemic species (i.e. native and restricted to an area). They may be the conservationists' bestfriend ([Solow, 1974](#); [Hannesson, 1983](#)), depending on specific, context dependent market and species characteristics, as a monopolist has an interest in restricting supply to increase prices, if consumers do not react too much (i.e. under limited demand elasticity). A vast range of market structures ([Damania and Bulte, 2007](#); [Hannesson, 1985](#)) sticking to real world situations have been studied. However, the full range of interactions between a species endemism, local market power, cost of effort and access to final consumer markets require more analysis to clarify the impact of market structure.

Other drivers of overexploitation can be found in the large expected benefits (relative to other local economic activity) some natural resources can bear, most of the time because of their rarity (i.e. absence of economically viable substitute), whether today or in the future ([Kremer and Morcom, 2000](#)). While the effects of substituting man-made products to disrupted ecosystem services are starting to get empirically studied ([Frank, 2024](#)) and show how dreadful costs can be, the effect of introducing substitutes to illegally poached wildlife products can be an example of strong substitutability between natural and man-made assets ([Chen, 2017](#)). As broader forces affect overexploitation, including poverty, it is clear that addressing overexploitation implies generalizing conclusion from the interplay of a single species with the institutional setting, how a species' future interacts with the availability of substitutes, and how the distribution of revenues from sustainable harvests may foster a reasoned use of the resource.

A wide range of policies have been implemented at different organisational

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<sup>39</sup>The notion of *carrying capacity* has been used since the mid-XXth century by population ecologists (for a history of the notion, see [Sayre \(2008\)](#)) to describe the maximum population size of a species a given ecosystem can sustain in the long run.

levels, to jointly or separately halt the identified drivers of biodiversity decline on land and at sea, with varying degrees of success.

## Biodiversity policies : from global to local

Successive international policy frameworks have sought to halt biodiversity loss by addressing its drivers comprehensively. In 2022, the 15th conference of the UN Convention on Biological Diversity launched the [Keunming Montreal Global Biodiversity Framework \(GBF\)](#), replacing the Strategic Plan for Biodiversity 2011-2020 and the Aichi Targets after the failure to meet its objectives<sup>40</sup>. The GBF sets four global goals for 2050, with 23 measurable targets to halt biodiversity loss by 2030. These goals include maintaining ecosystem integrity and connectivity and preventing human-induced extinctions (Goal A), sustainably using biodiversity (Goal B), sharing conservation benefits and burdens equitably (Goals C and D)<sup>41</sup>. [Targets](#) include restoring 30% of degraded ecosystems, conserving 30% of land and sea areas, and ensuring the sustainable use and management of wild species.

Other international treaties, such as the [Convention on International Trade in Endangered Species \(CITES\)](#) established in 1973, regulate trade in endangered species to prevent illegal wildlife trade<sup>42</sup> and promote species survival. Despite its scope, CITES' effectiveness is debated. Local enforcement ([Heid and Márquez-Ramos, 2023](#)) and demand reduction campaigns ([MacFarlane et al., 2022; Moorhouse et al., 2024](#)) are critical, but trade bans can sometimes increase prices and poaching incentives ([Hsiang and Sekar, 2016](#)). In some cases, conservation farming has succeeded by "flooding the market" ([Gentry et al., 2019; Phelps et al., 2014; Tensen, 2016](#)). Supply-side interventions have occasionally succeeded at reducing poaching and recovering wild populations – i.e. vicuña and spotted cat ([IUCN, 2000; Sahley et al., 2007](#)) – but they have also failed – i.e. green python, African elephant ([Lyons and Natusch, 2011; Hsiang and Sekar, 2016](#)). Uncertainty around conservation outcomes from market-based approaches has led to

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<sup>40</sup>Among the 20 Aichi Targets, none were globally met in 2020, and only 6 were partially met including the identification and eradication of invasive species on islands, the setting of 17% of terrestrial and inland water areas and 10% of coastal and marine areas as conservation areas, the implementation of policy instruments and effective national biodiversity strategy and planning, and the increase in financing biodiversity protection. Reasons invoked for the failure were the lack of clear indicators to assess targets, and no obligation to report on progress towards achieving the targets ([Maron et al., 2021](#))

<sup>41</sup>See [Section G. Kunming-Montreal Global Goals for 2050](#)

<sup>42</sup>CITES features 183 member parties (countries), it lists species across "appendices", with varying degree of protection of the species and restrictions limiting the trade in endangered species. Appendix 1 : the most endangered species, threatened with extinction and prohibited international trade, except when the purpose of exports is not commercial

Appendix 2 : species that are not necessarily now threatened with extinction but that may become so unless trade is closely controlled

Appendix 3 : species included at the request of a Party that already regulates trade in the species and that needs the cooperation of other countries to prevent unsustainable or illegal exploitation

continued reliance on trade bans and controls that are often ineffective at reducing poaching.

National and supranational policies have also been key. In the U.S., policies like [Wilderness Act of 1964](#) created protected areas to preserve habitats. In the wake of the environmentalist movement of the 1960s and 1970s, landmark regulations aimed at protecting natural habitats, such as the [Clean Water Act of 1972](#) (ensuring sewage to limit the disruption of wildlife habitat), and specifically targeted towards species conservation with the [Endangered Species Act of 1973](#). Results of the Endangered Species Act are debated. While the impacts seem to be overall positive on species recovery, budget dedicated to listings are slim, and the associated costs are substantial and concentrated on private landowners while benefits are more broadly distributed ([Brown and Shogren, 1998](#); [Langpap et al., 2018](#)). Localized initiatives, such as the [Yellowstone Yukon Conservation Initiative](#) (1993), connect ecological areas across the U.S. and Canada, using private conservation schemes and local policy making. In Europe, the Natura 2000 network<sup>43</sup> has created the largest conservation area globally, covering 18% of land and 9% of marine regions in the EU, across 28,000 sites. In broad strokes, it delineates conservation areas of ecological interest where development and human activities are restricted. Its ambition stemmed from taking into account the scale of biodiversity processes rather than administrative boundaries to develop an interconnected network of conservation areas. The ecological and economic performances of such a network are substantial, as they generate spatial spillovers both in terms of economic and ecological performance ([Cocco et al., 2023](#)).

Acknowledging that biodiversity habitat can be seen as a continuum between unsuitable and suitable conditions, mechanisms such as Payments for Ecosystem Services (PES) are leveraged to incentivize conservation on agricultural land. Taking into account the ecological spillovers of decreased spillovers, payments for ecosystem services with agglomeration bonuses, such that neighbors gain an additional marginal benefit when a new local participant implements conservation measures, can be efficient ([Parkhurst et al., 2002](#); [Bareille et al., 2023](#)). Overall, the spatial consequences of decentralized policies has yet to be fully integrated in policy making.

Finally, some policies aim at mitigating the threats posed by climate change on ecosystems and species, by changing landscape connectivity. In mediterranean forests, where biodiversity is exceptionally high but wildfires are an ever growing threat ([Dupuy et al., 2019](#); [Wasserman and Mueller, 2023](#)), fuel treatment operations<sup>44</sup> limit the occurrence and severity of wildfires. Public policy is leveraged in

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<sup>43</sup>A system of protected areas, established in application of the European Union Birds Directive (1976) and Habitats Directive (1992), and formally in place starting the mid 2000s

<sup>44</sup>Mechanical thinning, prescribed burns, and sometimes, logging, have been leveraged to decrease the fuel load in risky areas and theoretically decrease the probability and severity of burns

the face of increasing risk, limited insurability and threats to biodiversity. For example, with limited insurability of homes in the wildland urban interface in California<sup>45</sup>, as well as the potential economy-wide human and non-human damages from wildfires (Wang et al., 2021; Heft-Neal et al., 2023; Ayars et al., 2023) state-mandated and operated fuel treatment policies are of the essence. However, with increased budgets and improved spatial planning, these policies could achieve better performances in reducing risk while protecting biodiversity.

Decentralized policy mechanisms exist, such as mandates to create a defensible buffer around individual properties : in California, a 100-foot defensible around houses is mandated in State Responsibility Areas, and can translate in reduced insurance premia; in France, in dedicated regions, the "obligation de débroussaillement" mandates fuel control operations in a 50m radius to "decrease the intensity of wildfires and limit their spread"<sup>46</sup> with fines reaching 5,000 euros for failing to comply.

I focus on the analysis of the interplay between biodiversity and human actions, through the NCPs it provides and the anthropogenic drivers of its decline. As existing policies have had varying degrees of success in halting biodiversity decline, a framework for policy design is required. I use a framework stemming from ecology and economics to jointly analyze the causes of this decline and provide policy recommendations.

## Biodiversity as an economic object

The definition of economics has expanded with new methods and objects but primarily focuses on analyzing human behavior at individual and collective levels to manage scarce resources across alternatives (Mankiw, 2011; Bade and Parkin, 2002; Backhouse and Medema, 2009). This leads to two goals: understanding and explaining the state of the world (positive approach) and determining the best ways to manage resources (normative approach). Economics thus provides tools to analyze biodiversity loss and design policy.

However, applying economics to biodiversity is challenging. It requires the commensurability of values, often through monetary valuation. Initially, biodi-

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upon wildfire occurrence. In numerous regions, such as conifer forests in California (Vaillant et al., 2009; Kalies and Yocom Kent, 2016; Low et al., 2023), eucalypt forests in South Western Australia (Burrows and McCaw, 2013; Boer et al., 2009; Florec et al., 2020), southern Europe (Fernandes et al., 2013), evidence shows that fuel treatments, can mitigate wildfire intensity and spread. Land management agencies have historically implemented these policies in Australia (Burrows and McCaw, 2013), Europe, and the United States (and are projected to ramp up, for example under the Infrastructure Investment and Jobs Act of 2021 in the US)

<sup>45</sup>For example, 200,000 homeowners will see an increase in their insurance premium by an average of 34.1% from Allstate insurance in November 2024. In 2023, the FAIR plan, designed to be the insurer of last resort in California (state mandated but privately funded) saw a 38.3% increase in its total exposure.

<sup>46</sup>Translated by the author - Article L131-10 of the Code Forestier

versity was valued for its products (hunting, fishing, logging) traded at market prices, focusing on resources in a specific state—dead. This approach captured only part of the "use value" of species (Krutilla, 1967) (in the NCP framework, the material NCPs associated with food and materials), failing to consider their full value. Over time, the notion of "use value" expanded to include species' direct and indirect contributions. Many studies have used market proxies to estimate biodiversity's price<sup>47</sup>. Where market proxies fail, for lack of data for example, non-market valuation techniques have emerged (Carson, 2012), relying on stated preferences<sup>48</sup> (i.e. declared rather than observed willingness to pay). With the ecosystem services framework, valuation techniques were scaled to capture various services (Costanza et al., 1997), including recent modeling global modeling efforts (Giglio et al., 2024). Multiple methods extended biodiversity valuation across scales, from genetics to habitats and functions (Bartkowski et al., 2015). Recently, approaches shifted from direct monetary metrics to assessing species' effects on outcomes like health (Frank and Sudarshan, Forthcoming; Frank, 2024). A significant body of research rejected monetary valuation, focusing instead on biodiversity metrics to weigh against economic outcomes (Mouysset et al., 2011; Wätzold et al., 2016). These metrics help assess or plan biodiversity evolution with a scientific measurement, rather than through incomplete monetary valuation.

Managing biodiversity involves balancing alternatives while accounting for the specificity of living elements, regeneration and extinction rates, which requires understanding its temporal dynamics. Economics provides a framework to model these dynamics and assess the impact of different actions on current and future biodiversity. Models, as "stories with structure" (Gibbard and Varian, 1978), where the structure is "the logical and mathematical form of a set of postulates" with "elements of interpretation" (Gibbard and Varian, 1978), are used for a variety of purposes (see box 3). Alongside the evolution of monetary valuation techniques, "bioeconomic" models have been developed to design policies for resource management and biodiversity conservation.

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<sup>47</sup>For instance, hedonic methods (Rosen, 1974) use variations in market prices for goods like real estate linked to environmental features, while the travel cost method (Clawson and Knetsch, 1967; Bhandari and Heshmati, 2010) measures consumer spending on experiences like wildlife viewing.

<sup>48</sup>For example, following the Exxon-Valdez spill in 1989, surveys were developed to estimate the value of affected biodiversity by asking people's willingness to pay for recovery (car, 1992; Arrow et al., 1993; Carson et al., 2003), though these methods are controversial (Diamond and Hausman, 1994)

### Box 3 - What do models do?

Varenne (2014) furthers the approach qualifying models as "mediators" between the real world and scientific thought, and labels models as "facilitators", across multiple dimensions. A non-exhaustive typology of the roles models can play includes (i) a pedagogical role (facilitating communication), (ii) a predictive role (facilitating anticipation), (iii) a heuristic role (facilitating the explanation of a mechanism with a few simple interactions), (iv) prescriptive (facilitating the response to a given problem) and (iv) integrative (facilitating exchanges between disciplines).

## Bioeconomic modeling for the study and management of biodiversity

Bioeconomic models are analytical tools (i.e. with a mathematical formulation) that jointly model the feedbacks between components of biodiversity in wild or weakly managed ecosystems and economic activities, at different levels (e.g micro, mezzo and macro levels). They blend together a decision model emerging from economic theory, and the dynamics of biodiversity elements from ecology. Bioeconomic models (Gordon, 1954; Smith, 1969; Clark, 1973) have emerged from joint efforts by economists and ecologists to manage resources accounting for the specific dynamics of biotic elements (Parent et al., 2024)<sup>49</sup> as truly interdisciplinary models (see box 4).

Historically, the first bioeconomic models have emerged from population ecology and static economic analysis, to study the management of fisheries. The Gordon-Schaeffer (Gordon, 1954; Schaefer, 1954) model highlights the evolution of a fish population according to different harvest regimes, and aims at maximizing revenues in equilibrium. It distinguishes effort levels between those providing the maximum economic yield (i.e. resulting in the economic profit) from those providing the maximum sustainable yield (i.e. resulting in the largest fish growth), yielding new policy perspectives: as the maximum sustainable yield effort is larger than the maximal economic yield, the policy target should be the latter. Aiming for the maximum economic effort would therefore yield larger fish populations and promote economic efficiency, compared to unregulated, open-access. The original model was later extended to account for transitory dynamics and integrate elements from capital theory, focusing on the dynamic allocation of resources through time (Smith, 1969; Clark, 1973).

In the 1970s, economic decision making was applied to the progression of

<sup>49</sup>As highlighted in Parent et al. (2024), the concavity of the "ecological production function" i.e. of landings, resulted from the application of the law of decreasing returns to human effort. It was only with Schaeffer's input that the concavity of the ecological production function in Gordon (1954) became grounded from an ecological point of view, stemming from a population dynamics argument (using a logistic growth function)

pests in forests and agriculture (Hueth and Regev, 1974; Feder and Regev, 1975), and the bioeconomic modelling framework was soon applied to study the optimal management of species, both goods and bads i.e. large game and forestry v. invasive pests, leveraging single population dynamics, without much spatial processes (Swanson, 1994; Skonhoft, 1999; Alexander, 2000; Horan et al., 2002). In the 1990s, a second strand of bioeconomic models started to focus on the optimal conservation of species at the community level to find the mechanisms to conserve biodiversity through habitat management, ranging from reserve design to agricultural policies to foster conservation (Costello and Polasky, 2004; Polasky et al., 2001, 2005; Wätzold et al., 2016; Mouysset et al., 2011). The two strands developed and progressively included advances from ecology, especially landscape ecology (see box 4) and spatial processes<sup>50</sup> and economics, with the impacts of uncertainty on decision making<sup>51</sup>, and the coordination of agents with competing interests and in non cooperative settings<sup>52</sup> (see chapter 1 for an in-depth literature review).

Overall, bioeconomic models have been used for a variety of uses, spanning all the uses highlighted by Varenne (2014) . While they have gradually included additional dimensions and intricacies, they still face challenges to address the drivers of biodiversity decline (Drechsler, 2020).

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<sup>50</sup>This literature was pioneered by Huffaker et al. (1992); Brown and Roughgarden (1997); Sanchirico and Wilen (1999) studied first strategic interactions and the open access dynamics of metapopulations, with spatial dependence of migration. Within the same framework, Sanchirico and Wilen (2005) study the optimal policies to regulate an open-access metapopulation fishery. Costello and Polasky (2008); Blackwood et al. (2010) sacrifice density dependence for the optimal management of goods and bads at a large spatial scale in discrete space. Brock and Xepapadeas (2010, 2020) develop models using continuous transport for species. Their method allows to circumvent dimensionality curses, but requires the management of partial differential equations.

<sup>51</sup>The natural resource management literature has examined how risk affects decision making with risk neutral perspectives (Reed, 1979; Costello and Polasky, 2008), risk and tipping (Costello et al., 2019) and risk averse perspectives (McGough et al., 2009; Kapaun and Quaas, 2013; Tahvonen et al., 2018). The full effect of different attitudes towards risk and consumption smoothing is a recent endeavor. Disentangling the effect of risk and time preferences, Quaas et al. (2019); Augeraud-Véron et al. (2019) characterize the insurance value of capital. Berry et al. (2019) analyze insurance and self protection in the context of ecological resources and endogenous risk. Recently, Kelsall et al. (2023) characterize the effect of preferences towards risk and intertemporal variability of income on resource extraction.

<sup>52</sup>In the wake of the seminal fish war contribution of Levhari and Mirman (1980), numerous contributions have investigated the management of resources in non-cooperative settings, such as Janmaat (2005); Kaffine and Costello (2010); Costello et al. (2015, 2017). Other strands of the literature have studied the management of resources in contexts of contrasted interests, such as conservation agents and agropastoralists, Skonhoft (1998))

### Box 3 - A brief overview of ecological modeling for biodiversity

Ecology is a branch of biology that studies of the relationships between living organisms and their environment.

Dating back to Humboldt (XVIIIth century) natural history and the enterprise to catalog the living realm, ecology took a turn with Darwin's work on species evolution through natural selection (*On the Origin of Species*, 1859) into evolutionary ecology.

Along the XXth century, ecology focused on the fluctuations of populations of given species, and started to use mathematical models of population dynamics (e.g. logistic growth, linking population level, growth and carrying capacity of the ecosystem [Verhulst \(1826\)](#)) and interactions across populations, like predator-prey dynamics (with the works of [Alfred J.Lotka \(1925\)](#) and [Volterra \(1926\)](#)).

In the middle of the XXth century, community ecology span from earlier studies in natural history, studied how communities change through time after disturbances, with pioneering work from [MacArthur and Wilson \(1967\)](#) studying the patterns of species richness in line with broader geographical features and metapopulation models studying the spatial patterns of species abundance ([Levins, 1969](#); [Roughgarden, 1974](#))

In the late XXth century, landscape ecology recognized the role of spatial patterns in ecological dynamics. The spatial arrangement of habitat patches became the focus of study, and methods started to include Geographic Information Systems (GIS) and spatially-explicit single and multiple species population models (metapopulation and metacommunity models), gradually viewing the landscape as an interconnected network of patches ([Hanski, 1998](#); [Urban and Keitt, 2001](#)), where stochastic (demographic, environmental, genetic) and extrinsic (habitat loss, persecution, competition with other species) cause affect spatially distributed populations ([Hanski, 1998](#))

Around the same moment, conservation ecology ([Soulé, 1986](#)) aimed at addressing biodiversity loss, and focuses on preventing extinctions and preserving species diversity. Tools started to include population viability analysis, extinction risks models and species distribution models.

## Modeling challenges to address overexploitation, habitat loss and fragmentation

As bioeconomic models are typically dynamic, have gradually included the effects of economic and environmental stochasticity<sup>53</sup>, they face general challenges, such as the inclusion of participatory approaches and indigenous knowledge<sup>54</sup> in their framing and resolution. Additionally, as most of the literature has focused on population dynamics for single species<sup>55</sup>, even in granular spatial models (Sanchez and Wilen, 1999, 2005; Costello and Polasky, 2008; Brock and Xepapadeas, 2010; Sanchez et al., 2010; Albers et al., 2010; Costello et al., 2017) (i.e. metapopulations or continuous space population transport models), the explicit modeling of communities through space remains a challenge, to fully characterize the evolution of diversity with policies. Focusing on habitat can help adopt a community perspective and overcome data limitations, using species area relationships (MacArthur and Wilson, 1967) although difficulties of aggregating habitat for different species subsist. However, specific community dynamics can be hindered by the use of proxies, and community level abundance and richness data should be used when possible.

Bioeconomic models need to account for different objectives. On the one hand, optimal biodiversity use and preservation must be studied, so we can design the relevant policies to reach it. On the other hand, bioeconomic models can be used to assess the comparative performance of policy outcomes when the immediate implementation of first best policies is impossible, and only second-best policies are available. Hence, a variety of models can be used for different objectives, but they should integrate possibilities to run second best analysis (Lipsey and Lancaster, 1956)

More specific challenges exist to address habitat loss, fragmentation and over-exploitation. Overall, the inclusion of space in bioeconomic remains a fruitful research avenue. As highlighted previously, the role of spatial heterogeneity and dispersal has gradually been included in the bioeconomic toolbox. However, the analysis of the endogenous determination of spatial connectivity and dispersal is yet to be accomplished<sup>56</sup>. This raises important technical problems. First, when space is discretized, the number of state variables increases drastically. For processes that are state-dependent (i.e. where decision depends on

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<sup>53</sup>Drechsler (2020) nevertheless highlighted that stochasticity remained an untypical feature of bioeconomic models

<sup>54</sup>"Dynamic bodies of integrated, holistic, social and ecological knowledge, practices and beliefs pertaining to the relationship of living beings, including people, with one another and with their environments", in the IPBES framework

<sup>55</sup>A notable exception is Brock and Xepapadeas (2002), who model the evolution of  $N$  species albeit without space

<sup>56</sup>A notable exception is Brock and Xepapadeas (2010) who endogenize the formation of ecological patterns in economics

the observation of state variables), the increase in the number of state variables leads to the notorious "curse of dimensionality" (Bellman, 1957), where dynamic programming fails. This requires technical adjustment for global solutions<sup>57</sup> as adapting the search space (Brumm and Scheidegger, 2017), or resorting to different solution methods such as neural networks for interpolation of the value function (Friedl et al., 2023). Fruitful avenues arise when space is described as a continuum and diffusion processes described using partial differential equations (Brock and Xepapadeas, 2010, 2020), although they raise complex mathematical issues. When space is discretized, increasing the spatial resolution of a model often comes at the expense of other dimensions, such as the temporal dimension, or the complexity of economic and/or biological processes<sup>58</sup>. Optimizing spatial interactions to maximize welfare can be challenging due to the presence of non-convexities. As demonstrated in Box 3, connectivity — defined as the relationship between habitat patches and their connecting paths — may exhibit non-convex behavior. In other words, connectivity may not increase linearly or smoothly as more patches or paths are added. Consequently, the objective function governing connectivity optimization may not be well-behaved, particularly when non-convex constraints are present. This can lead to difficulties in finding global optima, as local solutions may not guarantee optimal welfare outcomes. Third, tools from landscape ecology, such as graph theory applied to ecological network is a fruitful, yet uncharacteristic feature of bioeconomic models (Drechsler, 2020)<sup>59</sup> to efficiently manage large spatial optimization problems.

This difficulty is increased when looking at strategic, non-cooperative settings (Levin et al., 2013). As a matter of fact, with state dependent dynamics, increasing the number of players is notoriously difficult. On networks, the determination of non-cooperative equilibria is difficult (Bramoullé et al., 2014), especially with endogenous networks and more than 1 strategic choice i.e. resource use and connectivity (Chen et al., 2018; Sadler and Golub, 2023). Increasing the heterogeneity among agent types is also important in understanding the drivers of connectivity and overexploitation (or under control). This is challenging, as non-symmetrical behavior can lead to tricky equilibrium determination, even in non spatial settings. Sources of heterogeneity can include ecological productivity and economic

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<sup>57</sup>Following Brumm and Scheidegger (2017), "global solutions" refer to "solutions computed utilizing equilibrium conditions at numerous points within the state space of a dynamic model", as opposed to "local solutions" which relies on "a local approximation around a model's steady state, as achieved through perturbation methods" from Friedl et al. (2023), p.1

<sup>58</sup>For example, Blackwood et al. (2010), ? develop extensive spatial models with linear growth (i.e. constant per capita growth), Costello and Polasky (2008) develop a model absent stock dependence on migration patterns, or Epanchin-Niell and Wilen (2012) develop a cellular automata model for pests spread in a integer programming framework, modeling presence of a species and not its extent and growth

<sup>59</sup>A notable exception is ? who consider a network of connected fisheries through graph theoretical measures to determine cost-effective protected areas with linear fish growth

costs and benefits, within functional forms, and across functional forms (for example, linear quadratic v. linear costs). With increased heterogeneity, analytical tractability becomes difficult, and bioeconomic modeling must resort to numerical methods. It is however key that models maintain a heuristic function (i.e. explain isolated phenomena) while increasing their prescriptive and predictive roles. In market strategic interactions, such as resource monopoly or duopoly, existing models from industrial organization are yet to be fully included ([Damania and Bulte, 2007](#)). Economic heterogeneity (such as different harvesting productivities or cost structures) among strategic actors is important to determine the resource evolution in a strategic setting.

## Research questions

In this dissertation, I focus on the role of 3 NCPs i.e. habitat creation and maintenance<sup>60</sup>, the regulation of organisms detrimental to humans<sup>61</sup>, and the provision by biodiversity of materials and assistance<sup>62</sup>, on land and at sea.

As I have exposed earlier, the major drivers threatening biodiversity (at different scales) and the provision of these NCPs are habitat loss and fragmentation, and overexploitation/under control. Existing policies have failed to halt the decline of biodiversity, and further scientific research can help refine policy design. Bioeconomic modeling provides a useful framework to integrate ecology and economics to guide policy, but faces several methodological challenges. Hence :

*What are the effects of endogenous spatial processes on the drivers of biodiversity loss? How can they be managed to mitigate the observed decline?*

*What are the effects of strategic behavior on the drivers of biodiversity loss?*

*How can bioeconomic models be refined to take into account these effects?*

## Dissertation outline

To answer these questions, my dissertation features 4 chapters, that tackle these research questions using different specific research questions and tools.

In the first chapter, I review the literature on bioeconomic models applied to the management of terrestrial social-ecological systems from a methodological

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<sup>60</sup>"The formation and continued production, by ecosystems, of ecological conditions necessary or favorable for living beings important to humans", ([Díaz et al., 2018](#)), Table S1

<sup>61</sup>"Regulation, by ecosystems or organisms, of pests, pathogens, predators, competitors, parasites and potentially harmful organisms"([Díaz et al., 2018](#)), Table S1

<sup>62</sup>"Production of materials derived from organisms in cultivated or wild ecosystems and direct use of living organisms for decoration, transport, company and labour", ([Díaz et al., 2018](#)), Table S1

and narrative perspective, to gain a general understanding of the field as well as the literature gaps that remained to be filled. In [Jean and Mouysset \(2022\)](#), we highlighted two main paradigms structuring the field, in the form of modern reappraisals of the conservationist/preservationist debate ([Banzhaf, 2019](#)) in the early 20<sup>th</sup> century. On the one hand, a "reasoned harvesting" paradigm studies the optimal use (or control) of monetary-valued resources and policies that enforce it applied to endangered species, invasive species and pests, and forestry, mostly studied by economists. On the other hand, a more recent "biodiversity conservation" paradigm focuses on the most cost-efficient way to conserve a variety of species, in weakly to strongly managed (i.e. agricultural) landscapes, which embrace a more interdisciplinary perspective. This chapter highlighted methodological challenges associated with bioeconomic modelling and knowledge gaps, which I used to develop the rest of my dissertation.

In chapters 2 and 3, I focus on the economics of habitat loss and connectivity, in terrestrial landscapes, and integrate space as a decision variable in bioeconomic models. Decision variables are spatially located (i.e. population size, quantity of habitat, costs etc), and subject to decision in relation to their surroundings : their location and their connectivity is at the heart of the decision problem. In the two chapters, connectivity structures different phenomena, sometimes conflicting objectives and triggers different policy mechanisms.

	Chapter 2	Chapter 3	Chapter 4
Habitat loss, fragmentation			
Overexploitation underharvest			

Table 3: Thematic divides of chapters

	Chapter 2	Chapter 3	Chapter 4
Decision maker	Social planner	Social planner, non-cooperative equilibrium	Non-cooperative equilibrium
Space	Small and large scale	Small scale	Absent
Planning horizon	5 steps, 10 steps	Infinite	Infinite
Type of heterogeneity	Network structural	Ecological and economic	Economic
Resolution method	Spatial heuristics	Analytical and numerical	Analytical and numerical
Data	Simulations	Simulations	Empirical
Biodiversity level	Community	Population	Population
Ecology perspective	Landscape	Population and landscape	Population
Measurement unit	Patch	Individuals (abundance)	Individuals (abundance)

Table 4: Model characteristics of chapters

In a second chapter, with L. Mouysset, we consider the management of landscape connectivity. We study the optimal spatial dynamic management of landscape connectivity in forest landscapes, when biodiversity habitat and wildfire risk and damages both depend on connectivity. In our model, *adolescent* forest patches foster biodiversity habitat, but as they grow into *mature* forest patches, they risk wildfire ignition. A social planner chooses the spatial allocation of fuel treatments dynamically, such that treatments in each patch reset the successional stage to *juvenile*, where wildfire risk and biodiversity habitat are absent: reducing wildfire risk harms biodiversity habitat. The social planner aims at minimizing the connectivity of wildfire risk-bearing patches, while maintaining biodiversity habitat connectivity, under a budget constraint. We adopt a landscape ecology perspective where forest patches are the unit to both measure biodiversity (habitat provided to a community) and wildfire risk. In our analysis, spatial state variables are discrete, and connectivity is a non-convex function : the incremental connectivity of a patch depends on the phenomenon considered (wildfire risk or habitat) as well as its surroundings. Additionally, the spatial optimization problem is made more complex with constraints on the set of treatable patches, because habitat connectivity matters. With this complicated objective, we can adopt a spatial perspective and circumvent the dimensionality curse ([Bellman, 1957](#)) by bounding the vegetation dynamics to 3 successional stages. In doing so, we show that repeated myopic optimization is equivalent to dynamic optimization on a 5 period planning horizon. We outline the production possibility frontier between the two objectives, and using a graph theoretic framework, we characterize treatment allocation rules at a small scale for general application. Unfortunately, small scale treatment allocation rules do not scale up to a larger dimension, leaving ample room for future work.

In the third chapter, I study the management of spatially distributed, mobile public bads ([Costello et al., 2017](#)). In this literature, the impact of directional patterns on optimal and non-cooperative management has been extensively studied. However, existing models mostly take movement as given, or dependent on relative population densities ([Huffaker et al., 1992; Bhat et al., 1996; Sanchirico and Wilen, 1999](#)), but do not consider how human decisions affect these movement patterns. Namely, the flow of species from one patch to another can be hampered by obstacles, i.e. conceptually, by fences : ecological networks feature a human layer, an endogenous decision process, and are not exclusively determined by ecological features. On the one hand, raising fences dissolves landscape connectivity and solves spatial externalities. In doing so, it promotes efficient control of bads, even in non-cooperative settings. However, in the presence of spatial heterogeneity (ecological or economic), it may be best to leverage these differences as arbitrage opportunities, to maximize welfare : bads could be corralled

where they are cheap to manage, or where they reproduce at a lower rate. In this chapter, I first characterize the optimal spatial management of a mobile public bad from a social planner standpoint in the presence of economic and ecological heterogeneities among patches. Then, I study the decentralized equilibrium in a non-cooperative setting, where landowners can build fences and control a pest. I show that while fences can solve the tragedy of the commons, the decentralized equilibrium may result in suboptimal allocation in the presence of ecological and economic heterogeneities, as spatial arbitrage opportunities are not exhausted.

In the fourth chapter, co-led with [J.Lawson](#), we study the fate of *Totoaba macdonaldi*, an endemic fish species in the Gulf of California in Mexico. *Totoaba* fishing and trade has been prohibited under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) for 50 years, recovering the population stock. Nonetheless, data indicates a significant resurgence in poaching. *Totoaba macdonaldi* is prized for its swim bladder on Chinese markets, and its trade is controlled by an organized crime group. Leveraging a wealth of new data, we revive the framework originated by [Damania and Bulte \(2007\)](#). We study if the control of totoaba by a vertical monopoly could be beneficial to the species. We find that results are sensitive to uncertain cost data, and analyze if substitution from aquaculture can provide a viable alternative. Unlike the original framework, we show that competition does not necessarily yield to stock collapse, and could significantly (-29%) reduce poaching and illegal profits (- 195 million \$ USD).

## Summary of publications and conferences

**Chapter 1 : Bioeconomic Models for Terrestrial Social Ecological System Management : a Review**, S.Jean and L. Mouysset, *International Review of Environmental and Resource Economics*, DOI : 10.1561/101.00000131

[Replication code](#) and [data](#) are publicly accessible

Presentations :

- European Association of Environmental and Resource Economists (EAERE) Annual Conference, Rimini, 2022
- ABIES Doctoral Days - Best Poster Award, 2022

**Chapter 2 : The Wildfire-Habitat Connectivity Dilemma: a Graph Theoretical Approach to Landscape Management**, S.Jean and L. Mouysset, *Working Paper*

[Replication code](#) and [data](#) are publicly accessible

Presentations :

- BINGO Seminar, CIRED, 2023
- Interdisciplinary PhD Workshop in Sustainable Development, Columbia University, 2023

**Chapter 3 : Fences - the Economics of Movement in Mobile Public Bads**, S. Jean, *Working Paper*

[Replication code](#) and [data](#) are publicly accessible

Presentations :

- PhD Seminar of the French Association of Environmental and Resource Economists, Université Savoie Mont-Blanc, 2024
- Parisian PhD Seminar in Environmental Economics, Nogent sur Marne, 2024
- CIRED Internal Seminar, 2024
- Biodiversity Economics Internal Seminar, iDiv, Leipzig, 2024

**Chapter 4: Little downside and substantial gains result from farming of To-toaba Macdonaldi**, J. Lawson, S.Jean (co-first authors), A. Steinkruger, M. Castellanos-Rico, G.M. Goto, M.A. Cisneros-Mata, E. Aceves Bueno, M.M. Warham, A.M. Sachs and S.D. Gaines, under review at *NPJ Ocean Sustainability*

[Replication code](#) and [data](#) are publicly accessible.

Presentations:

- BIOECON Network Annual Conference, University of Santiago de Compostela, 2023
- Trade and the Environment, Paris Saclay Applied Economics, 2023
- European Association of Environmental and Resource Economists Annual Conference, University of Leuven, 2024

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# Chapter 1

## Bioeconomic models for terrestrial social ecological system management: a review

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It is slightly modified to account for minor errors and add several references.

We present a cartography of 319 bioeconomic models applied to terrestrial habitats, combining quantitative analysis of methodological criteria and the narratives behind the equations. Using Multiple Correspondence Analysis and clustering, we identify four groups. Two adopt a conservation focus: the first emphasizes cost-effectiveness in preserving species without monetizing biodiversity, while the second focuses on habitat-based conservation, particularly in agriculture and forestry. The other two groups focus on harvesting, monetizing biodiversity to maximize agent utility and raising cost-benefit issues. One group focuses on endangered and invasive species, while the other highlights forestry. Temporal analysis reveals a recent decline in bioeconomic models for terrestrial social-ecological systems. We discuss this in relation to correlative and data-driven models and propose future challenges for mathematically-based bioeconomic models to reduce uncertainty and incorporate diverse frameworks.

**Keywords :** Biodiversity; land use change; maximum economic yield; mathematical model; ecological economics; environmental and resource economics; natural capital; ecosystem services; multiple correspondence analysis; K-modes clustering

**JEL codes :** Q57, Q23, Q24;

# 1 Introduction

Implementing sustainable development constitutes one of the main challenges of the 21st century, given the current ecological crisis. In the last fifty years, two successive trends have paved the way for ongoing studies in sustainability issues. Beginning in the 1970s, large-scale pollution betrayed many of the pressures exerted on the environment by anthropogenic activities. This was followed in the 1990s by a new trend that highlighted the impact of the ecosystem on human development and economic activities (Costanza et al., 1997). The idea that an ecosystem could affect economics yielded new concepts such as the well-known concept of *ecosystem services* (Daily et al., 1997; Hassan et al., 2005; Bateman et al., 2013). The current understanding of sustainability combines these two perspectives, as reflected by the concept of *sustainable development*, which is defined as the management of a complex system, namely, a *social-ecological system* (Ostrom, 2009), and which articulates human society and the ecosystem (Dasgupta, 2008). This dual concern notably led to the creation of the International Panel for Biodiversity and Ecosystem Services (IPBES<sup>1</sup>).

Managing these social-ecological systems, therefore, requires understanding the co-evolution of society and ecosystems. On a more technical note, designing sustainable development paths in the context of the ecological crisis requires identifying sustainable dynamics or equilibria, defined as the long-term states needed to maintain viable both socioeconomic and ecological systems. To characterize such sustainable states and their underlying drivers, an adequate understanding and representation of the relationships between society and ecosystems are required. In this respect, we are forced to deal simultaneously with considerations of economic and ecological dynamics as well as their mutual interactions in interdisciplinary-opened scientific researches. Different modeling frameworks that probe the relationships between ecosystems and economics have already been developed in the literature with the economics of natural resources (for an overview, see Halvorsen and Layton (2015))

The integration of natural resources in economics models started with the management of exhaustible resources (Hotelling, 1931; Dasgupta and Heal, 1974). Typically, economic models have been developed to study the extraction of fossil energy. In these settings, natural resources are characterized by a regeneration rate negligible in comparison with its extraction rate. The central economic question about such an exhaustible natural resource regards the investment of the

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<sup>1</sup><http://www.ipbes.net/> - "The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) is an independent intergovernmental body established by States to strengthen the science-policy interface for biodiversity and ecosystem services for the conservation and sustainable use of biodiversity, long-term human well-being and sustainable development" see <https://ipbes.net/about>

rent emerging from extraction into a non-natural asset. The extraction rate thus depends on the interest rate: the larger the interest rate, the faster the extraction. Besides these models, other economic models have been dedicated to exploring the management of renewable resources (Smith, 1968; Plourde, 1970; ?). Contrary to exhaustible resources interpreted as a stock, renewable resources are modeled as a flow. Indeed, renewable resources are characterized by commensurable rates of regeneration and extraction. Economic models thus investigate how to maintain the balance between the regeneration and extraction rates, and how to avoid large extraction rates, which would unbalance ecological dynamics and yield to resource erosion. Because biodiversity is a typical example of renewable resources, such resource models are usually designated as bioeconomic models (Gordon, 1954; Scott, 1955).

Historically, bioeconomic modeling for renewable resources (Clark, 1973b; Kontoleon et al., 2007) has extensively been developed for fisheries. Mathematical models of species extinction have been developed on Gordon's and Schaeffer's fisheries models (Gordon, 1954; Schaefer, 1954) to examine the conditions under which the eradication of a given species might appear to be the most attractive policy for a resource owner. Clark's work, which has popularized the concepts of Maximum Sustainable Yield (MSY) and Maximum Economic Yield (MEY), provided a crucial framework for policy-making in regards to exploited marine resources. Typically, these equilibria show that economic decisions that account for interactions between ecosystems and economics reduce the fishing effort compared to decisions taken in ignorance of these interactions. Many extensions of these fishery models have been specifically developed to introduce complexity into the ecological and economic processes (see Petrakis et al. (2012) for a review), towards ecosystem-based fishery management. The development of bioeconomic mathematical modeling for renewable resources in the case of fisheries can probably be explained by the fact that marine biodiversity has been one of the first ecosystems to be strongly damaged by anthropogenic actions. For example, the North Sea herring population collapsed from more than 2 million tons to less than 50 000 tons in the 70s due to overfishing, (Nash and Dickey-Collas, 2005). This marine decline clearly affected economic activities: in the UK alone, the value of the herring fishery dropped from 14 to 2 million pounds between 1977 and 1979, before a slow recovery (Wood and Hopper, 1984).

However, the intensification of anthropogenic pressures over all the ecosystems for the last 50 years, combined with a substantial improvement in the knowledge about ecosystems, has called for bioeconomic studies on other types of biodiversity and habitats (such as estuarine, aquatic or terrestrial habitats). Among them, terrestrial biodiversity is of special interest due to its competition for land with humans. Indeed, urbanization (McDonald et al., 2008; McKinney, 2008) and

agricultural land-use changes ([Dudley and Alexander, 2017](#); [Reidsma et al., 2006](#)) over the last decades have been identified as major drivers of the erosion of terrestrial biodiversity. Such land uses are responsible for the degradation of habitat quality, thus altering species nesting success and survival.

In spite of some early models focusing on pest management in agricultural settings ([Hueth and Regev, 1974](#); [Feder and Regev, 1975](#)), bioeconomic models have been widely developed for the management of non-marine social-ecological systems 20 years after their application to marine resources. Considering such a development of the literature, several reviews have tried to summarize its findings. Some of them adopted an explicit public policy perspective: for example [Boyd et al. \(2015\)](#) focus on bioeconomic model-based articles which investigate conservation planning and the use of return on investment measures or [Epanchin-Niell \(2017\)](#) who reviewed bioeconomic models about the management of terrestrial invasive species. While these studies review the policy issues and the solutions brought by bioeconomic models, they lack methodological consistency since they use a variety of elements, such as narratives, methodological traits, and mixing methodological and statistical approaches. These reviews thus fail at giving an overview of a single methodological framework applied to the management of terrestrial social-ecological systems. On the opposite, other reviews consider a methodological perspective about the bioeconomic modeling framework. We can notably cite [Eppink and van den Bergh \(2007\)](#) which study the biodiversity indicators and theories underlying bioeconomic modeling, as well as [Castro et al. \(2018\)](#) who explore the methodological advances in bioeconomic models applied to agriculture (and mostly abiotic elements) and [Drechsler \(2020\)](#) who explores the integration of spatiality, dynamics and uncertainty in "ecological economic models" for the management of biodiversity and ecosystem services. If these reviews bring valuable insights on the bioeconomic modeling fields, they usually fail in providing a quantitative assessment of the field, with a notable exception in [Drechsler \(2020\)](#). Moreover, these studies often disregard the analysis of the narratives deployed with the mathematical specifications.

In this article, we aim at providing a cartography of the bioeconomic models applied to terrestrial biodiversity based on quantitative methods by combining mathematical and narrative elements of the modeling frameworks. To do so, we performed a review of 319 articles fitting with our specific focus on mathematical and process-based bioeconomic models as popularized for fisheries, but applied to wild and weakly managed terrestrial biodiversity (agro-biodiversity which is strongly managed by humans has been excluded since it has been widely reviewed by agricultural economics). We then studied our database through a methodological perspective by combining an analysis of the methodological criteria included in the economic model, the ecological one and their linkage, and

an analysis of the narratives underlying the equations. In this way, we adopted Gibbard and Varian's standpoint ([Gibbard and Varian, 1978](#)), on stories as an integral part of the model in economics. We provide a cartography of our database using a quantitative analysis relying on Multiple Correspondence Analysis and clustering techniques. Our cartography is organized in 4 groups that we depict in terms of methodological and narrative specifications. More precisely, two of them adopt a conservation perspective: while the first one focuses on how to efficiently preserve species given a limited budget through a cost-effectiveness approach without any biodiversity monetarization, the second one stands for a second generation of models tackling habitat-based conservation measures with specific applications in agriculture and forestry. The last two groups are concerned with the notion of harvesting. Biodiversity is monetized and the problem is framed as the maximization of the utility (or profit) of agents, derived from the flow of the biodiversity variable raising thus a cost-benefit problem. While the notion of harvesting is mostly applied to endangered species and invasive species in one group, a specific interest for forestry characterizes the second one. Surprisingly, the method exhibits a recent and on-going decline over the last years. In regards with this result, some elements of discussion regarding the competition with neighbouring methods, especially the correlative and data-driven models, are in investigated. Since the IPBES methodological report ([IPBES, 2016](#)) highlights the need to maintain a diversity of modeling frameworks to investigate the management of social-ecological systems, especially to embrace different understandings and decrease uncertainty, a discussion on the future of the mathematically-based bioeconomic models is therefore of special interest. In this perspective, we conclude by providing some challenges for its development.

## 2 Review method

### 1 Article selection

We performed bibliographic searches on SCOPUS using a wide array of keywords regarding bioeconomic models for renewable terrestrial resources (see annex E for the specified query). Based on these, we ruled out all the articles applied to marine ecosystems. Furthermore, as [Eppink and van den Bergh \(2007\)](#), we tracked the references of the selected articles by hand, and used the website [Connected Papers](#), which provides a map of the earlier and derivative papers from an article. This first screening provided approximately 1000 articles. Then we refined our article selection by precising the concepts of *model* and *bioeconomic*. Figure 1.6 illustrates the process.

First, we need to precise the definition of *model* we used for this review. Indeed

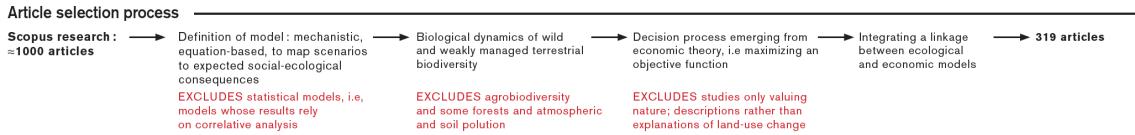


Figure 1.6: Article selection process for inclusion in the systematic review

the modeling literature usually mixes scenarios and models which are both used to provide information to support policy and decision making. However they refer to two different modeling components: scenarios describe plausible futures for drivers of change and options for altering the course of these drivers through policy and management interventions while models enable scenarios of change in drivers to be translated into expected consequences for social-ecological systems (IPBES, 2016). Adopting a methodological perspective of the field instead of a public policy one, we will focus here on models only. Nevertheless, different types of models coexist in the literature. They can rely on quantitative relationships between the components of the social-ecological systems, or on qualitative relationships between them. While the first ones usually have mathematical foundations, the second ones are expert-based. In those models, the experience of experts and stakeholders, including local and indigenous knowledge holders, is used to describe relationships. In consistency with the bioeconomic models popularized by Clark about fisheries, we restrict our attention to quantitative models. Eventually, the scientific literature distinguishes 2 types of quantitative models. On the one hand, the correlative models which rely on empirical data and estimate values for parameters through statistical relationships. In these models, processes are rather implicit. Second, the process-based models which describe explicitly-stated processes or mechanisms based on established scientific understanding. In these models, model parameters therefore have a clear and predefined interpretation. The scope of our review focuses on process-based bioeconomic models. This is of special interest since correlative modelling is probably the best known to manage social-ecological systems, especially due to the popularity of correlative species distribution modelling (Elith and Leathwick, 2009). In such a context, we postulate that a specific focus on the alternative method might bring new insights about social-ecological system management.

Second, bioeconomics is a polysemous term which is used in different strands of literature: a first group is related to N. Georgescu-Roegen and develops a thermodynamics understanding of social-ecological systems (Georgescu-Roegen, 1971); a second group, led by Clark on Gordon's and Schaeffer's foundations, develops mathematical models integrating ecological and economic processes (Clark, 1973a,b; Gordon, 1954; Schaefer, 1957)<sup>2</sup>; finally a third group is related

<sup>2</sup>See Parent et al. (2024) for a history of the ‘standard’ fishery model, notably the gradual inclusion of dynamics

to biomimetism where technological innovations are inspired by living systems ([Van Lancker et al., 2016](#)). In this review, we focus on the second group of literature, related to Clark's bioeconomic mathematic modeling.

To do so, we define bioeconomic models at the intersection of 3 conditions:

1. integrating an explicit biological dynamic
2. integrating a decision process emerging from economic theory,
3. integrating a linkage between ecological and economic models.

The first item characterizes the ecological dynamics of a renewable resource where the rates of regeneration and extraction are commensurable. Except for this condition, no specific requirement of the ecological process at play is needed. Different ecological processes such as population dynamics or niche distribution are thus eligible. By biological, we mean that the dynamics have to be related to living organisms. In other terms, the stake of the model has to be related to biotic elements. This condition aims at excluding pollution models or carbon and nitrogen models ([Nordhaus, 1994](#); [Lemoine and Traeger, 2014](#)). Eventually, by explicit we mean mathematically formalized. This condition is necessary to exclude exclusively declarative bioeconomic models (*i.e* bioeconomic frameworks without any mathematical formulation). Indeed, the objective of this study is focused on changes in a specific method (*i.e* the mathematical process-based bioeconomic model) rather than in a problem (*i.e* the bioeconomic one). Because they adopt a different methodological framework, correlative or declarative bioeconomic studies need to be excluded from our corpus.

The second item precises the economic side of bioeconomic models. By considering an economic decision process, we aim at excluding articles performing an economic valuation of biodiversity such as empirical studies giving the monetary values of species, like owls or bats ([Montgomery et al., 1994](#); [Penn et al., 2019](#)). Although such studies are highly valuable to deal with the ecological crisis, they stem from a very different methodological tradition (choice experiments and monetary valuation). By explicitly requiring a decision process from economic theory, we ensure to avoid agro-ecological models. Indeed, many agro-ecological models address the question of sustainable management of terrestrial social-ecological systems and bring valuable knowledge to this question. However, they combine ecological dynamics with land-use change models without specifying the economic determinants of these land-use changes (some costs are sometimes associated with these land-use changes but without being driven by economic processes) ([Sabatier et al., 2010](#)). The methodological corpus we are interested in in this article is rooted in economic theory. Thus, we only consider economic decision models, in which agents allocate scarce resources to fulfill their

objectives. Agents can, for example, maximize their utility or profit, or act as cost-minimizers to achieve specific goals.

The third condition is that of an integrated ecological-economic system, *i.e.*, how the ecological and economic models are coupled. This bioeconomic linkage is not specified and can take different forms: for example, it can be mutual (by considering simultaneously the anthropogenic effects on ecosystems and the economic valuation of biodiversity in an economic problem) or unidirectional (one of the two effects mentioned above), and it can be done by prices or by physical variables. If the bioeconomic coupling is done by prices, economic value will be granted to the biodiversity elements to make them commensurable with other economic determinants. However, this monetary quantification has to be incorporated into a decision model (cf previous item).

Eventually, these bioeconomic modelling specifications have been applied to terrestrial social-ecological systems. Since many studies take place in an agricultural context, it is necessary to specify here the distinction between *agro-biodiversity* and *agricultural biodiversity*. *Agro-biodiversity* stands for species which are directly managed by farmers (for examples the crops species, the battle species etc) while *agricultural biodiversity* stands for wild biodiversity living into agricultural habitats (such as birds, bats etc). Because the economic aspects of agro-biodiversity have been broadly studied by agricultural economics, we focus here on wild terrestrial biodiversity. In this perspective, bioeconomic models applied to only managed forests, such as the seminal article of [Faustmann \(1849\)](#)<sup>3</sup>, are excluded. Models with natural forest ingrowth are however in our scope. To finish, we formally exclude articles with marine case studies. For example, articles with both marine and terrestrial case studies have been excluded in this review. In doing so, we aim at providing a restricting view about terrestrial social-ecological system management. However the integration of such excluded articles appears as a natural perspective of future extensions of this work.

Based on these criteria, we individually screened all the papers selected in the first look to refine our database. Among 1000 articles identified after the first literature screening, we selected 319 articles developing bioeconomic models applied to terrestrial social-ecological systems.

## 2 Analytical framework

To analyze mathematical tools such as bioeconomic models, we adopted here a methodological perspective. However as mentioned by Gibbard and Varian ([Gibbard and Varian, 1978](#)) at an early stage, stories are an integral part of the model in economics. More precisely, the authors explain that a model is a *story* with a

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<sup>3</sup>Moreover, Faustmann's work focusing on tree values does not feature any biological dynamics.

*specified structure*<sup>4</sup>. In that perspective, methodological specifications are not sufficient to characterize the model since the questions the authors want to explore and the stories they can tell with it are at the core of the model identity. Such narrative elements are more than chronicles, they are essential to connect economic modeling research with the specifics of the world (Morgan, 2001). Without these narrative elements, it is impossible to apply model-structures directly onto the facts of the economic world. Since we are interested in models that are motivated by concrete stakes such as resource management, the biodiversity crisis and sustainable development, exploring narratives associated with the methodological specifications of the mathematical model is crucial to characterize the outline of such a bioeconomic modeling.

In this context, we developed an analytical framework based on two dimensions: the first one is based on a set of methodological criteria related to mathematical equations, while the second one is related to the narratives associated with the mathematical tool. Based on the combination of these two dimensions, we aim at providing an overall cartography of bioeconomic modeling as a tool to investigate the management of terrestrial biodiversity.

### 3 Cartography method

For our methodological analysis, we first investigated a set of 18 criteria related to the ecological model, the bioeconomic linkage, and the economic model.

#### 1 Ecological criteria

The ecological criteria aim at precising how biodiversity is captured by the ecological model. To do so, we mobilize 8 criteria split into 2 groups. The first group of criteria helps to understand the paradigm of biodiversity while the second group is related to the technical specifications of the ecological model.

Within the first group, the first criterion is related to the measure of biodiversity. Indeed, biodiversity can either be modeled *per se* (for example based on population dynamics models) or be deducted from a proxy (typically, the habitat suitable for biodiversity or economic activity). The second criterion precises the proxy measure: this proxy can be habitat, economic activity, a conservation budget, or not be specified. The third criterion precises the ecological state variable in the ecological model. More precisely, the biodiversity variable can be related

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<sup>4</sup>"A model [...] is a story with a specified structure. The structure is given by the logical and mathematical form of a set of postulates, the assumptions of the model. The structure forms an uninterpreted system [...] Although the term 'model' is often applied to a structure alone, we shall use it in another sense. In economists' use of models, there is always an element of interpretation: the models always tells a story." (Gibbard and Varian, 1978), p.666)

to the individuals (such as in population or metapopulation models), the species (when focusing on species richness), or the community, when both species abundance and richness are taken into account. The fourth criterion focuses on the type of biological diversity, *i.e.* we distinguish functional and genetic diversity definitions. Finally, the fifth criterion characterizes the biodiversity level at which the model intends to contribute. Some articles are focused on a single species (for example, articles based on a population model developed for one species) while some others adopt a community perspective by integrating a pool of species. In some cases, when species interact, models display two species. However, many of the articles we reviewed did not focus on species interactions and therefore encompassed a larger number of species. This community perspective can be either explicit, as in articles modeling populations of different species, or implicit, in studies using a habitat proxy as a biodiversity measure and informing about the community living in this habitat. It is interesting to note that there is no systematic implications between habitat, proxy-based models and community level contribution since the habitat might be related to one single species.

Besides this first group of criteria for the characterization of biodiversity, we mobilize a second group of criteria related to the ecological technical specifications. The first criterion is related to the category of biological dynamics: we distinguish population dynamics models (such as in the seminal model developed by Clark, or articles implementing age-structured modeling) and other ecological dynamics. These other dynamics can be for example either a niche distribution model or Brownian motion models. The second criterion characterizes the spatial dimension of the ecological process. Spatial considerations can be explicit when the ecological process implies spatial exchanges (typically a metapopulation model) or implicit, when the ecological process at play takes place in a heterogeneous context (for example when heterogeneous patches are taken into consideration for an aggregated analysis without any exchange between the patches). Eventually, the spatial dimension can be absent. Then the third criterion is related to the integration of stochasticity in the ecological modeling. Stochastic components may include dispersal probabilities of species across land patches as well as probabilities of species extinction.

Table 1.A sums up the ecological criteria with their related items.

## 2 Bioeconomic linkage criteria

Bioeconomic linkage criteria characterize how biodiversity is taken into account in the economic model and the economic decision. To do so, we mobilize 3 criteria. The first criterion indicates whether the biological element has been monetarized or not. In order to make biodiversity commensurable with other economic

variables in the decision problem, some articles rely on an economic valuation of biodiversity (in other words, biodiversity is expressed in monetary units, such as dollars). A monetary bioeconomic linkage occurs in two situations: either if the study is directly driven in monetary terms (for example when biodiversity is measured through a proxy in economic units) or if the ecological model is developed in non-monetary terms (with a biodiversity measure *per se* or based on a habitat-based proxy) but the biodiversity is monetarized thanks to a monetarization method to be integrated into the economic decision.

The second criteria precises how the bioeconomic problem is raised. We distinguish two problems: the cost-benefit problem and the cost-effective problem. Cost-benefit analysis integrates costs and benefits related to classical economic factors and ecological factors, then selects the decision which maximizes the overall utility. Due to criticism on monetarization methods ([Diamond and Hausman, 1994](#)), some authors favor cost-effectiveness analysis which separates classical economic factors and the ecological ones. The economic decision is thus taken according to a maximization under constraints. Typically, the optimal decision maximizes the profit or the utility under an ecological constraint. By isolating ecological and economic objectives, this cost-effectiveness method aims at limiting the substitutability between natural and non-natural capital. Interestingly some studies consider the ecological value in economic terms (for example when biodiversity is measured through an economic proxy) but keep separated the benefits or costs emerging from the ecosystem and the ones emerging from classical economic factors. In other terms, an economic value for biodiversity does not necessarily imply a cost-benefit problem. It is the reason why it is informative to keep in our review the two criteria, relative to biodiversity monetarization and the bioeconomic problem respectively.

The third criterion captures the position of the biodiversity stake in the bioeconomic model. The biodiversity stake can be within the objective of the maximization such as in cost-benefit problems but also in a cost-effectiveness problem which maximizes the ecological output while satisfying a cost constraint. Then, the biodiversity stake can be a constraint (in a cost-effectiveness problem which maximizes profit under ecological constraint for example). Eventually, other stakes occur either when the biodiversity stake emerges in both the maximization and constraint or when the biodiversity stake is an output. The simultaneous consideration is possible when are considered different taxonomic groups (one being in constraint while the other is included in the maximization) or when non-human well-being is taken into consideration in the objective function while biological dynamics constitute mechanistic constraints. The biodiversity stake can be assessed as an output computed after the economic decision.

Table 1.A sums up the bioeconomic linkage criteria with their related items.

### 3 Economic criteria

Economic criteria specify the economic side of bioeconomic models. More precisely, we explore a set of criteria related to the technical economic specifications. They are related to dynamics<sup>5</sup> and spatial dimensions, and to uncertainty. Bioeconomic models are economically either static or dynamic. Similarly to ecological technical specifications, we explore the spatial and uncertain dimensions. Economic spatiality can be investigated explicitly through a spatial process such as trade between regions or implicitly by spatial heterogeneity of economic variables, or eventually absent of bioeconomic models. Eventually, economic models can be either deterministic or stochastic if an economic variable is primarily subject to a source of uncertainty.

To finish, we explore four last criteria regarding the general characteristics of bioeconomic models. The first one is related to the solving method used to explore the bioeconomic question. We distinguish 3 forms of solving method in the articles of our corpus: closed form resolution, numerical resolution and the combination of both. The second criterion informs whether the study is empirical or theoretical or whether its combines empirical and theoretical perspectives. Additionally, we explore how the model is used to highlight the economic question. If the solution emerging from the bioeconomic model characterizes a judgement on the best behavioral options or policy instruments, the model use is normative. On the other hand, if a paper investigates some behaviors of the system without any recommendation, the model use is descriptive. Eventually, we characterize whether the model is framed in terms of general equilibrium or partial equilibrium.

Table 1.A sums up the economic criteria with their related items.

### 4 Methodology-based cartography

These methodological criteria have been analysed through a Multiple Correspondence Analysis (MCA). MCA allows to uncover the underlying structure of categorical data by performing a recombination of the data into a two-dimensional space formed by orthogonal vectors which maximize the variance (inertia) explained by the data (see [Benzécri \(1976\)](#) for seminal works and [Roux and Rouanet \(2010\)](#) for a modern presentation).

As MCA can be sensitive to unbalanced variables (*i.e.* variables whose distribution are highly skewed towards one value), we performed a sensitivity analysis to select the optimal combination of variables to use in the MCA, based on the ex-

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<sup>5</sup>Indeed whereas our definition of bioeconomic models requires a condition of dynamics in the ecological model (see section 1), we do not impose any dynamics specifications on the economic side to be included in the database.

plained variance. To do so, we performed an MCA analysis with all the possible combinations of our sample. The graph 1.C in appendix G exhibits the explained variance as a function of the number of criteria. Among the 18 methodological criteria, we selected the set of 14 methodological criteria (see tab. 1.A) which keeps a large set of criteria while reaching 31% of the explained variance. The rationale for variable selection was to avoid redundancies as well as excluding variables that are too skewed and would impair MCA analysis.

Based on these selected criteria, we performed a classification with a K-modes algorithm ([Huang \(1998\)](#)). The K-modes algorithm generalizes the K-means method<sup>6</sup> to categorical data, and uses a dissimilarity measure to assign observations to clusters. One of the inconvenients of K-modes algorithms is the need to specify the number of clusters. Therefore, the number of groups used in the classification was determined using a cost function, namely the sum of the within variance of each clusters. We used the so-called 'elbow-method' ([Ketchen and Shook \(1998\)](#)), stating that the optimal number of clusters is located at an elbow of the curve relating the sum of the within cluster variances and the number of clusters. Indeed, after this point, the reduction in the sum of the within cluster variances becomes less important, suggesting additional clusters do not significantly improve results. Figure 1.D in appendix G depicts this cost function. For the following analysis, we will consider the optimal cluster of 4. However since 9 clusters might also be considered as optimal clustering, we also present an MCA classification with 9 clusters as robustness test (see figure 1.E in appendix G).

## 5 Narrative-based analysis

In order to perform a narrative analysis, we used the titles, keywords and abstracts of the papers in our database. Then we pre-processed the data by removing stopwords and grouped similar words together (for example, *farming*, *farmers* and *farms* were all grouped under *farm* with this procedure). Moreover, because our analysis relies on single words, typical nominal groups were recoded (for example, *endangered species* was recoded into *endangeredspecies*)<sup>7</sup>. For our analysis, we kept words which occurred at least 5 times in our database<sup>8</sup>. Since we have 319 articles, we thus kept a significant portion of the words database, which

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<sup>6</sup>The K-means algorithm ([MacQueen, 1967](#); [Lloyd, \(1957\)](#)) is a standard classification algorithm in Natural Language Processing. Documents are mapped to a vector space featuring as many dimensions as there are distinct words in the document, and are thus coded in a binary fashion. The algorithm picks random initial centroids, computes the Euclidean distance to other observations, which are assigned to the closest clusters. Centroids are thus actualized, and the procedure is repeated. If no observations changes cluster upon a new iteration, it converges.

<sup>7</sup>The following expressions were recoded and grouped together : endangered species, bio-economic, invasive species, ecosystem service, optimal-control, dynamic-programming, integer-programming, cost-effective, cost-benefit, reserve-design, optimal-management, land use, property rights, conservation-planning

<sup>8</sup>These 5 occurrences can come from a single article or at most 5 articles.

displays the most information. More precisely, a total of 1202 words out of 4355 relevant words (27.6%) were kept, accounting for 81% of word occurrences.

Eventually, we classified words according to semantic fields. Based on the 1202 words words kept for the analysis, we designed 8 lexical groups, pertaining to two habitats (agricultural and forest), two species status (invasive species and endangered species), two management semantic fields (policy and risk) and two human-nature paradigms (conservation and harvesting). The list of words in each semantic field is depicted in appendix F. In order to characterize the narratives underlying the different groups resulting from the methodology-based classification, we investigated the bias of each semantic fields into them. More precisely, for each methodology-based group, we assess the ratio between the frequency of the semantic fields and the number of papers included in this group. This ratio avoids size effects between groups.

## 4 Database overview

### 1 Temporal and geographical distributions

Figure 1.7 presents the distribution of the articles in the database. Most articles range from the 90's, testifying the recentness of the use of such methodology for terrestrial social-ecological systems. Except some early-bird articles published in the 70's related to the management of agricultural pests and pesticides use ([Hueth and Regev, 1974](#); [Feder and Regev, 1975](#)), the distribution of the articles follows a Gaussian function with a 20-years spike between 1995 and 2015. This indicates that the use of such bioeconomic models to investigate the sustainable management of terrestrial social-ecological systems has decreased recently. This decline is of special interest as the question of sustainably managing terrestrial social-ecological system is far from solved. This situation is quite unusual for a methodology associated with such a burning issue which calls for a strong research effort and generates a huge amount of literature.

To complete this temporal distribution, we investigate the geographical origins of the authorship of the 319 articles (fig. 1.8). We observe that our database in majority emerges from North American and European research even if the part from Oceania is not negligible. Eventually a small part comes from Asia and Africa. This relative dominance of North American research could be explained by the original diffusion of Schaeffer's (American) and Clark's (Canadian) seminal models. From a more naturalist stand, the magnitude of the resources and the early conservation movement in North America could have paved the way for this trend.

However with a higher pressure on land use and land use change in Europe

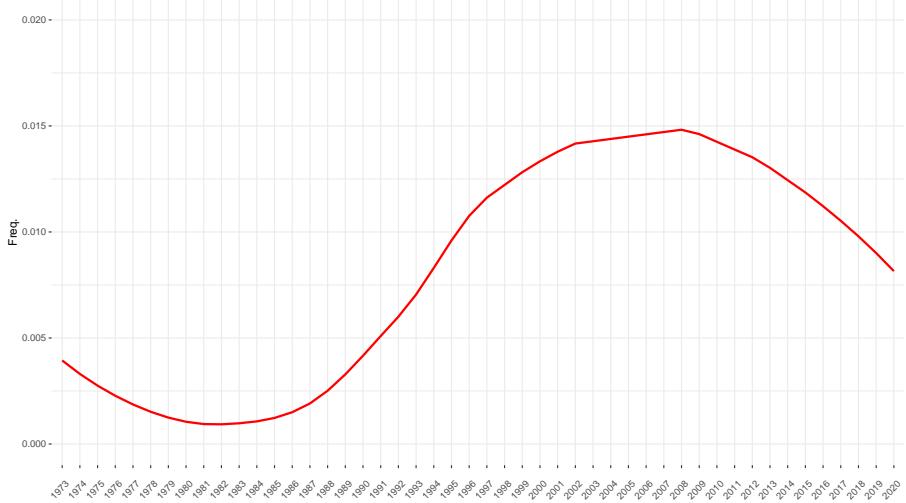


Figure 1.7: Temporal distribution of articles in the database.

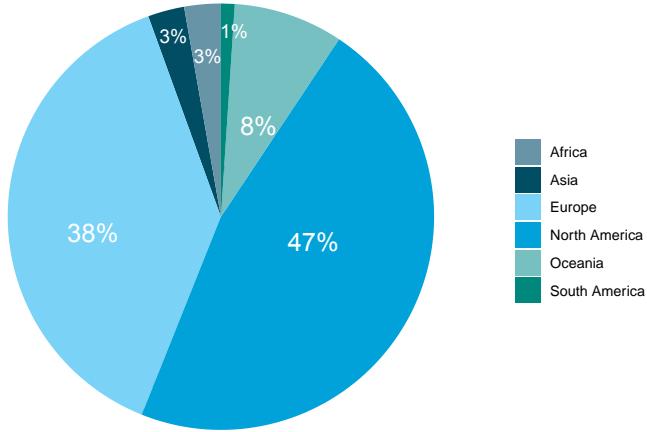


Figure 1.8: Geographical distribution of articles in the database.

than in the USA, European researchers look also very active to face the urgent and concrete stake of managing terrestrial ecosystems while reconciling socioeconomic goals and ecological requirements.

## 2 Journal and discipline distributions

The articles emerge from 97 journals which are related to different disciplines such as applied mathematics, economics, ecology and sustainability sciences (see tab. ??). Based on the journal affectation, table 1.1 sums up the frequencies of these 3 disciplines among our corpus of 319 articles.

We observe that most of the articles have been published in journals related to economics (60%) confirming the anchorage of bioeconomic modeling as an eco-

Table 1.1: Distribution of journal across fields

Field	Count	Percentage
Economics	190	60%
Ecology	83	26%
Sustainability science	34	10%
Applied Mathematics	12	4%

nomic approach. Among the journals, one of them captures a substantial part of the papers: 44 papers (*ie* 14% of the overall database and 23% of the papers published in economic journals) are indeed published in *Ecological Economics*. This dominance was expected since the methodology brought by bioeconomic modeling fits perfectly with the scope of the journal. Indeed, this journal focuses on the articulation of ecological and economic issues in the perspective of sustainable development<sup>9</sup>. Beside this journal, bioeconomic models contribute to classical resource management questions (with environmental and energy journals such as *Environmental and Resource Economics*, *Journal of Environmental Economics and Management*), applied questions and notably agricultural economic journals (such as in the *American Journal of Agricultural Economics* or the *Agricultural Economics*), theoretical economic questions (with classical theoretical journals such as *Econometrica*, *American Economic Review*).

The proportion of articles published in non-economic journals (40%) testifies an interest for bioeconomic models beyond its economic expected arena. The non-negligible part of articles published in Ecology journals (such as *Ecological Modeling*, *Conservation Biology*, *Ecology Letters* or *Journal of Theoretical Biology*), sustainability sciences journals (such as *Natural Resource Modeling*, *Agricultural Systems* or *Environmental Modeling and Software*) and applied mathematics (*Journal of Mathematical Analysis and Applications* and *Journal of Mathematical Biology* for example) emphasizes an acceptance of bioeconomic models outside the field of economics. And more specifically, it confirms a certain legitimacy of bioeconomic models regarding ecological theory and knowledge. In this perspective, bioeconomic modeling embraces a genuine interdisciplinary aspiration.

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<sup>9</sup>The scope of *Ecological Economics* mentions that "The journal is concerned with extending and integrating the understanding of the interfaces and interplay between "nature's household" (ecosystems) and "humanity's household" (the economy). Ecological economics is an interdisciplinary field defined by a set of concrete problems or challenges related to governing economic activity in a way that promotes human well-being, sustainability, and justice."

## 5 Database cartography

### 1 Methodology-based classification

Figure 1.9 presents the results of the Multiple Correspondence Analysis (MCA) running on 14 methodological criteria. It also displays the classification of the articles resulting from our K-modes algorithm into 4 groups : group 1, in green, with 47 articles; group 2, in purple, with 48 articles; group 3, in yellow, with 162 articles; group 4, in black, with 62 articles.

We observe on figure 1.9 that the MCA is well structured on both sides of the  $y$ -axis with groups 1 and 2 on the right side, and groups 3 and 4 on the left side. The  $x$ -axis offers a split between groups 1 and 2 while it does not strongly play on the groups 3 and 4 even if the main part of group 3 tends to be below the  $x$ -axis while the main part of group 4 tends to be above. Figure 1.E in appendix G exhibits the MCA based on 9 groups. While being more fragmented, the cartography exhibits a similar structure to the 4 groups classification.

The interpretation of the 4 groups comes with figure 1.10 which depicts the distribution of the items of the selected 14 methodological criteria. The colors stand for the contribution of the items to the structuration of the axes. We observe that the  $x$ -axis is strongly driven by the criteria related to the bioeconomic problem e.g. biodiversity monetarization, data anchorage, solving method and spatiality. More precisely the left side is characterized by a cost-benefit problem where biodiversity is monetized. The problems are theoretical and solved with closed-form solutions. Eventually, the problems do not integrate spatiality. On the contrary, the right side is characterized by the cost-effective problem where biodiversity is not monetized. The problems are mainly empirical and solved with numerical tools, and take into account spatiality. The  $y$ -axis is mainly driven by the integration of spatiality in the economic model and the framing of the economic problem as a general equilibrium.

Combining figures 1.9 and 1.10, we understand that the MCA classifies the articles in our database in a first group (in green) specified by a cost-effective problem, an absence of biodiversity monetarization, empirical and theoretical studies and stochasticities being present both in ecological and economic models ; a second group (in purple in figure 1.9) specified by a cost-effective problem, an absence of biodiversity monetarization, empirical studies and spatiality being explicit on the economic side and implicit on the ecological side ; a third group (in yellow in figure 1.9) specified by a cost-benefit analysis, biodiversity monetarization, numerical and theoretical solving and the absence of spatiality ; a fourth group (in black in figure 1.9) specified by a cost-benefit analysis, biodiversity monetarization, theoretical solving and explicit spatiality.

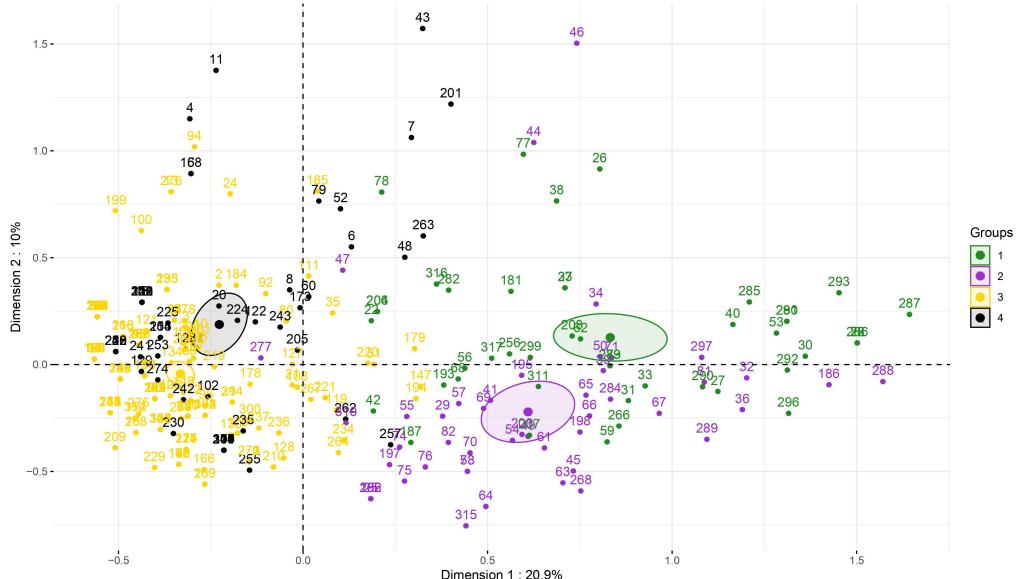


Figure 1.9: Multiple Correspondence Analysis (MCA) running on 12 methodological criteria and 4 clusters (K-modes)

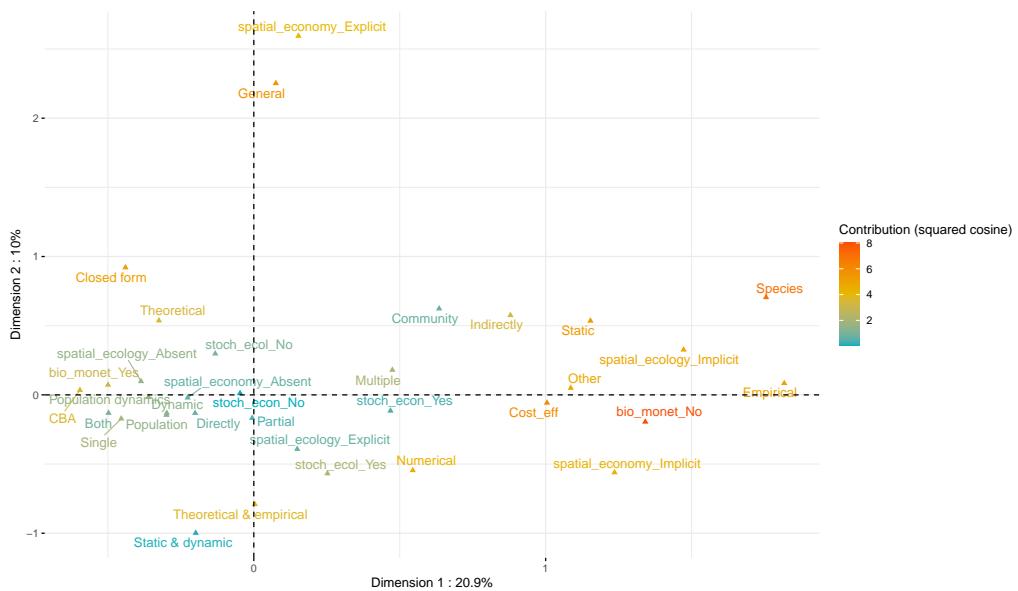


Figure 1.10: Distribution of the values of 14 methodological criteria among the MCA axes.

## 2 Narrative-based specifications

In order to interpret the narratives of the 4 methodology-based groups, we depicted on figures 1.A and 1.B the distribution profiles of the 50 most frequent words for each group.

First of all, we observe that for all profiles the most common words are those which are in common with the 4 groups. We identified the following keywords: (i) economic, cost, (ii) management, policy, strategy, conservation (iii) biodiver-

sity, resource, species, population, ecological, biological, (iv) model, optimal, dynamic, (v) land use, forest, habitat. This observation indicates that the 4 methodology-based groups are driven by a common narrative which regards an economic problem of management of biodiversity and natural resource and land use change based on models, mostly relying on optimal control theory. This result confirms the consistency of our database regarding the research question investigated in the selected papers within the database.

Since the specific words are too disparate to be easily understandable, we completed these profiles by a semantic fields analysis in order to characterize the 4 methodology-based groups. The figure 1.11 depicts the frequency of the different semantic fields in each group<sup>10</sup>. We observe that groups 1 and 2 are related to conservation issues. Among conservation-related articles, the ones with specific applications into agricultural landscapes, especially related to public policy issues, are preferentially located in group 2. On the opposite, groups 3 and 4 are related to harvesting issues. A specific focus on endangered and invasive species characterizes group 3. Eventually, group 4 looks dedicated to the risk problematic with forestry applications.

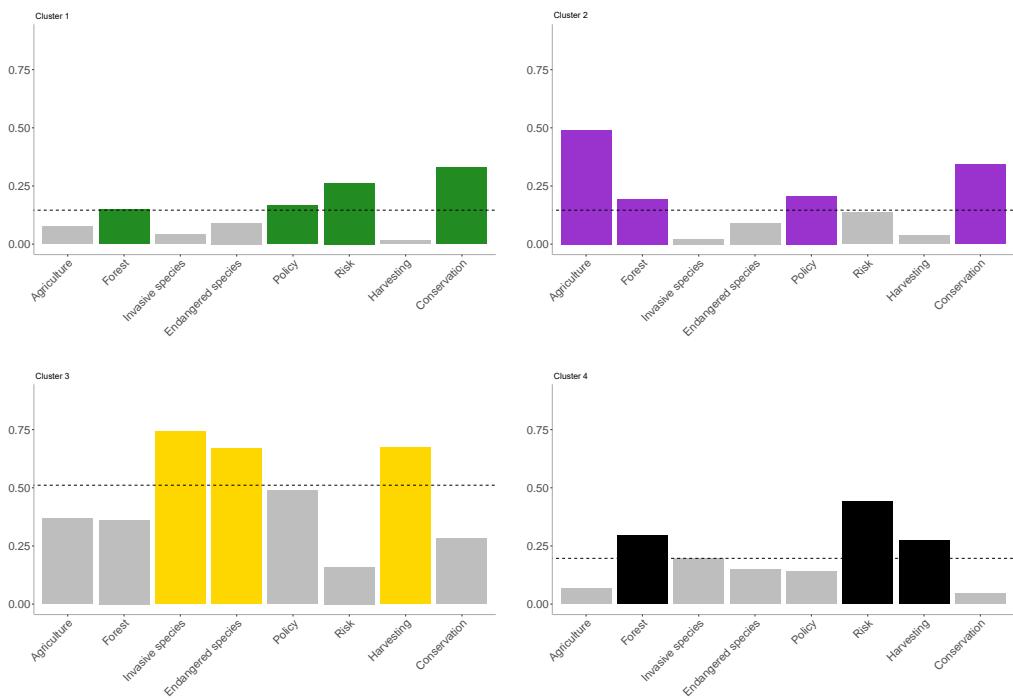


Figure 1.11: Frequency of the different semantic fields in the 4 methodology-based groups.

On the *y* axis is the proportion of mentions of lexical groups in a given cluster across all the mentions. The dashed line represents the size of each cluster as the share of articles of the database they represent. Each color corresponds to the cluster color in figure 1.9

<sup>10</sup>see appendix F for the listing of words within each semantic field

### 3 Overall cartography

Combining methodological and narrative specifications draws thus a 4-groups cartography where each group can be described as follows.

**The first group** is polarized towards conservation issues broadly rather than specifically applied to a type of habitat. Spanning from 1992 to 2019, with a median year in 2006, it can be viewed as a first generation of models applied to conservation, i.e, focusing on the optimal ways to conserve species rather than harvesting them. This corpus focuses on how to efficiently preserve species given a limited budget for land acquisition through a cost-effectiveness approach without any biodiversity monetarization. It can be viewed as a generalization of the so-called "Noah's Ark" problem ([Weitzman \(1998\)](#)). In this paper, Weitzman considers the genetic diversity of an array of species to maximize the amount of biological diversity one can fit into an Ark, e.g, given a limited budget and the cost of conserving a species. An array of papers, such as [Courtois et al. \(2014\)](#) revisit Weitzman's definition of diversity, including species interactions, to refine the criterion to be maximized in conservation planning.

Considering not only one Ark, but a variety of habitat patches for species conservation broadens again the issue. Moreover, including costs in the decision process is required to design efficient conservation strategy. This concern yields optimal reserve site selection problems. Whereas the seminal Weitzman's Ark framework was a theoretical one, this extension usually comes with a theoretical enquiry and an empirical case study. For example, [Costello and Polasky \(2004\)](#) focus on the optimal combination of sites suitable for an array of species that need to be set aside from development, permanently or temporarily. Using dynamic integer programming, the authors showed that the timing of decisions, the quality of habitat in patches as well as their costs is key to designing optimal reserve sites for a large set of Southern California vertebrates. Using the same approach, a wide array of papers focus on the static problem of optimal reserve site selection at a very large scale, in order to prioritize conservation projects. For example, [Moore et al. \(2004\)](#) focus on the minimization of the costs to operate a network of reserves in Africa that covers 10% of its 118 ecoregions. Using species-area relationships and considering that land costs are correlated with high endemism or threat, focusing only on cheap areas was unlikely to yield the desired conservation outcome. Moreover, factoring in land prices in the reserve site decision problems was shown to increase the cost-effectiveness of the prioritization scheme.

**The second group** spans from 1993 to 2021, with a median publication year in 2010. Focusing on conservation, it can be viewed as a second generation of models tackling specific habitat-based conservation measures. The typical re-

search question is how to conserve biodiversity in a working landscape, i.e, when land-use is devoted to agriculture, and to a lesser extent, to forestry. Considering biodiversity, mostly in the form of multiple species, as a separate entity, a cost-effective problem is framed in order to find optimal solutions to reconcile the economic and ecological objectives. In this context, a wide array of solutions are considered. For example [Polasky et al. \(2005\)](#) develop a spatially explicit framework in which a large set of vertebrates from Oregon can stochastically migrate across land patches as they compete for habitat with agriculture and forestry. Due to the analytical complexity of the problem, [Polasky et al. \(2005\)](#) use a variety of algorithms to gradually increase the biodiversity objective and find the least-cost policy in terms of land use, thus resulting in a production possibility frontier. While land-use policies are key, other articles investigate monetary based policy instruments to conserve biodiversity. In this approach, [Drechsler et al. \(2007\)](#) develop a single-species, spatially explicit meta-population model of butterflies living in an agricultural landscape in Germany. Taking into account species dynamics, agricultural constraints, and heterogeneous land quality for agricultural and conservation purposes, they design means of determining cost-effective solutions to biodiversity conservation through conservation payments. Based on this framework, they show that patch-specific conservation payments can increase ecological benefits up to 50% compared to uniform strategies. Co-leading a European strand of literature on the conservation of species in a working landscape is [Mouysset et al. \(2012\)](#). In this paper, a spatially explicit model of 620 small French agricultural areas is coupled with a public decision maker who aims at preserving diversity under budgetary constraint. Farmers decide their management schemes under uncertainty and with no specific regards to biodiversity, apart from economic incentives. The model is used to evaluate various policy scenarios pertaining to farm management and the impact on common farm bird species. Optimal policies such as tax and subsidies to promote biodiversity conservation are derived.

**The third group** is the largest group (51% of our database) from our classification, spanning over the whole temporal distribution (1973-2021) and a median year in 2005. It is mostly concerned with the notion of harvesting, i.e, removing a portion of the biodiversity variable for beneficial use. The measure of this beneficial use tends to be monetary, and the problem is framed as the maximization of the profit or utility of a set of agents derived from the flow of the biodiversity variable, mostly population, raising thus a cost-benefit problem. The notion of harvesting is mostly applied to two particular sets of species, endangered/remarkable species and invasive species, that are characterized with opposite properties : the former is an economic "good", the latter is an economic "bad".

In the endangered/remarkable case, a good example is ?. Considering the case of African wildlife, especially large mammals, and factoring in land-use costs, non-consumptive benefits, nuisance costs and harvest profits, Skonhoft examines the dynamics of a single species' population and its optimal harvesting scheme, in a deterministic framework. This paper can be seen as one of the most refined versions of the work of [Cla](#) and later on [Swanson \(1994\)](#), who examines the optimal harvesting of African elephants in the context of land-use pressures, later on refined by [Alexander \(2000\)](#) through the integration of non-consumptive values. In this strand of literature, the institutional arrangements between stakeholders are refined, thus examining the equilibria between poachers and locals, the potential for tourism revenue, and the interaction of conservation measures and harvesting. What is key is the Human around interactions surrounding the resource, rather than the resource's intrinsic dynamics, such as migration or uncertain population dynamics.

Invasive species, whether present in agricultural, forestry or wildlife settings, are one of the earliest application cases of bioeconomic modeling for terrestrial ecosystems. In these settings, a resource owner (mostly farmers or foresters) are concerned with the spread of a single invasive species. In this case, optimal control methods are developed to compute the optimal amount of surveillance and detection, pesticides use, preventive cuts or harvests, to prevent damages from invasions. A typical example can be found in [Jayasuriya et al. \(2011\)](#). In this article, a state of the art population dynamics, seed-bank model is applied to a crop invader. This invasive species spreads stochastically, depending on both its intrinsic growth rate, and the agricultural crop growth rate. Using dynamic stochastic programming, the authors show that control measures are always beneficial, and that if eradication is too costly, it still pays to maintain infestation at low levels. While agricultural damages are of interest, the value of ecological degradation from biological invasions are also considered. For example, [Taylor and Hastings \(2004\)](#) investigate the spread of *Spartina Alterniflora*, an invasive grass species, in Willapa Bay in the state of Washington in the USA. This species, subject to a density-dependent, age-structured growth function, is to be removed, and the authors investigate the least cost strategy, for the sake of the preservation of the local landscape.

Eventually, **the fourth group** spans all over our temporal distribution, with a median year in 2002. This group focuses on more specific biodiversity dynamics. It tends to focus on uncertain biodiversity dynamics, and to a lesser extent, multiple species relationships (mostly predator-prey, but incorporating some mutualistic configurations). In this context, decision makers are concerned with the optimal harvesting of a stochastic population that can be an economic good or

bad. It is therefore no surprise that forestry economics are more represented in this setting. A typical example can be found in [Lin et al. \(1996\)](#), where a density-dependent stochastic growth model governs the evolution of forest stands characterized by their diversity. The question, akin to Faustmann's seminal interrogation ([Faustmann, 1849](#)), sums up to when is it optimal to harvest this uneven-aged stands forest? Taking into account age and species diversity modifies the optimal harvesting rule.

Forests can also be the habitat to stochastic populations of invasive species. For example, [Epanchin-Niell et al. \(2014\)](#) focus on bark beetles and wood borers, that may invade forests. The authors focus on the optimal surveillance strategy to develop in order to prevent a detrimental forest invasion in New Zealand. The program's costs are weighed against the benefits (in the form of forgone damages) from earlier detection. Their appraisal of the relative costs and benefits from surveillance suggest that implementing the program is always beneficial, under all considered scenarios. Eventually, a small last strand of literature of this fourth group focuses on the economic implications of the stochastic nature of biodiversity on the provision of ecosystem services. Using a single species, closed-form mathematical framework, [Augeraud-Véron et al. \(2019\)](#) investigate the value of biodiversity as an insurance device for agricultural production, as it decreases agricultural productivity volatility. In a similar fashion, [Baumgärtner \(2007\)](#) characterizes the insurance value of biodiversity in the provision of monetary values ecosystem services, not specifically agriculture. Biodiversity conservation therefore becomes a financial product, akin to financial insurance.

Not surprisingly, articles from the first two groups (related to conservation paradigm) were published in economics journals for a first half, and non-economics journals for the second half (mainly Ecology journals but also Sustainability science journals). This testifies of the explicit integration of other disciplines in the study of conservation issues, while modeling approaches remain anchored by the economics methodology. On the contrary, articles from the last two groups (related to the harvesting paradigm) display a disciplinary distribution skewed towards Economics journals. This dominance of economics journals is consistent with the methodological specifications of the bioeconomic models within these corpus, which are directly in line with economic theory.

Eventually, the second group of our overall cartography displays an over-representation of European researchers (63% of the corpus, compared to 37% of the database) as well as an under representation from North-American research. A European strand thus emerges out of this corpus, led by Drechsler, Wätzold and Mouysset<sup>11</sup>, focusing on biodiversity conservation in agricultural settings.

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<sup>11</sup>These authors are the top 3 of the most credited authors in the corpus, thus each representing

The other corpus do not display a significantly different geographical distribution from the full database.

## 6 Discussion

### 1 Bioeconomic models as tools to manage social-ecological systems

Designing sustainable development paths in the context of the ecological crisis requires identifying sustainable dynamics or equilibria, which could be defined as the long-term behaviors needed to maintain both socioeconomic and ecological systems. To characterize such sustainable states and their underlying drivers, an adequate understanding and representation of the relationships between society and ecosystems are required ([IPBES, 2016](#)). In this respect, we are forced to deal simultaneously with considerations of economic and ecological dynamics as well as their mutual interactions by integrating feedback effects and interdependences between the ecological and socioeconomic systems ([Carpenter et al., 2009](#); [Figueiredo and Pereira, 2011](#); [Perrings, 2011](#)). Since the modelling communities in the natural and social sciences are relatively isolated from each other, substantial research efforts have to be done to overcome linguistic, epistemological, technical and other hurdles between the disciplines to provide a consistent framework ([Rindfuss et al., 2004](#))

The bioeconomic mathematically-based method reviewed in this article fits perfectly with this objective. By modelling complex structures and interactions within social-ecological systems, this type of model investigates how people perceive their well-being, how people make decisions to enhance their well-being, how it is affected by environmental conditions, how people may adapt their behaviour as their environment changes and how policies might be designed to be ecologically and economically efficient and socially accepted.

The set of models we reviewed in this article reveals nevertheless a plurality in the way that individuals and groups value nature, especially pending on contexts and scales. By combining methodology-based and narrative-based analysis, our cartography showed that this plurality of understandings, to perceive the interactions between human and nature within the social-ecological systems, can be embodied within two main and opposite human-nature paradigms. The first one is related to harvesting while the second one to conservation.

The harvesting paradigm resonates with the early nature paradigm where nature is mainly seen as wild nature, grasped in its emblematic dimension. In this

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10% or more of the publications.

context, living elements are linked to socioeconomic decisions without considering any of their ecological features nor economic particularities except their direct and visible benefits. It can be understood as the modernization of the "conservationist" movement in the United States in the late XIXth century, championed by Gifford Pinchot, who conceived Nature through its instrumental value for humans and adopted a model of rational planning for resource use ([Banzhaf, 2019](#)). This conception of nature underlies international institutions such as the World Wide Fund for Nature founded in 1961 or emblematic public policies such as the Endangered Species Act established in 1973 in the USA.

Beside this harvesting paradigm, the conservation group derives from a second paradigm stemming from the early "preservationist" movement, whereby Nature should be conserved for its own sake, led by naturalist John Muir ([Banzhaf, 2019](#)). This paradigm was reshaped by the concept of biodiversity in the 90's. Popularized in 1992 by the United Nations Earth Summit in Rio, the concept of biodiversity captures both the notion of biological diversity and its ongoing situation of crisis ([Robin and Libby, 2011](#)). This new concept has implied two switches. First, it appears crucial to extend the conception of biological diversity by incorporating genetic, population, and ecosystem diversity to the classical species diversity, and by moving from emblematic nature to common and ordinary nature. Second, such an explicit context of ecological crisis calls unambiguously for protection.

Today both paradigms coexist in the mathematically-based bioeconomic modeling framework. In this perspective, this method seems to offer an up-to-date and promising context to think and assess the management of terrestrial social-ecological systems. In the 1990's and 00s, the biodiversity crisis spurred social demand and agenda setting in environmental policy, thus accelerating the development of this method.

## 2 Discussion about the recent and on-going decline

Despite a large increase in the 90's and 00's, our review reveals a decline over the last few years (since 2008), which is surprising as the question of sustainably managing terrestrial social-ecological systems is far from being solved. Indeed this situation is quite unusual for a methodology associated with such a burning issue and which seems to offer an up-to-date framework. This recent decrease might suggest a lag between the questions opened by the sustainable management of terrestrial social-ecological system and the answers brought by this bioeconomic mathematical modeling method. Understanding such a lag constitutes a determinant methodological stake with two implications: (i) defining the insights of the bioeconomic methodology to the knowledge in the field of economics, (ii)

identifying perspectives of development of this methodology in regards with this ecological crisis.

A crucial perspective to investigate these questions is to proceed to a similar analysis of the neighboring methodological corpuses, including agro-ecological and land use change models, declarative bioeconomic models, simulation-based models (*i.e* without mathematical specifications, biodiversity and ecosystem service quantification articles etc). Studying the technical features of such methods and their changes would be a determinant piece of information to understand the coexistence of the different methods aiming at studying the management of terrestrial social-ecological systems. To complete this analysis, it may be informative to extend this overall comparative analysis to the habitat, by distinguishing marine and terrestrial habitats<sup>12</sup>. Indeed the nature paradigm might slightly differ among these habitats, due to differences in the intensity of the competition between nature and society. The most adequate methodology to investigate the bioeconomic question can thus be different. This might be an explanation of the differences in the development of such a methodology for marine and terrestrial resources

Among the neighboring methods, one of them merits specific attention, namely the correlative models (see for example [Leclère et al. \(2020\)](#), who use a wide array of Integrated Assessment Models (IAMs) and biodiversity models (BDMs) to evaluate biodiversity decline scenarios). This method, widely popular in ecological sciences, also fits with social expectations for decision-makers regarding social-ecological system management ([IPBES, 2016](#)). Indeed, there is a social demand for data-driven models since these ones look more realistic and reliable to make management decision. In this perspective, the correlative approaches based on large datasets might look more accurate to design concrete public policies and management strategies than the process-based model such as the mathematical bioeconomic models. Moreover, the IPBES report highlights the need for user-friendly modeling tools to be successfully used by decision-makers. Correlative models are based on mathematical tools since statistical analysis relies on mathematical foundations. However, by emphasizing the results on the data instead of the mathematical foundations, such tools look more understandable than process-based approaches which emphasize the equations of processes and frequently provide results in terms of stylized facts. By emphasizing the central-

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<sup>12</sup>Terrestrial bioeconomic models applied to terrestrial biodiversity management seem to represent a smaller yet comparable share of the literature as bioeconomic models applied to marine ecosystems. A search on SCOPUS yields 418 articles (respectively 212) against 407 (respectively 229). (We used the following query : *TITLE-ABS-KEY (bioeconomic AND model)* as well as *TITLE-ABS-KEY (bioeconomic AND modeling)* selecting the appropriate keywords pertaining to both sub-fields. Because the selection was operated using keywords, some articles applied to marine ecosystems can remain. The aim of these numbers is to gauge the magnitude order of the different literature strands

ity of mathematics in the method, the process-based models are less accessible to a non-specialist audience. These specificities might explain the relative decline of mathematical bioeconomic models which may have benefited integrated data-driven approaches.

Despite substantial advantages, data-driven correlative approaches have to deal with several difficulties. First, they usually rely on specific and user-friendly softwares. While many tools are open-source and freely accessible, access to proprietary softwares can be attained through financial support from funding sources such as the UN, the World Bank and the Convention on International Trade in Endangered Species ([IPBES, 2016](#)). Similar problems emerge to access some datasets since some of them remain costly. To overcome this difficulty, it is possible to use different platforms collecting biodiversity and ecosystem services datasets at large scale. However their use is not always easy since inconsistencies and a lack of complementarity persist and interfere with an optimal use of the data. Second, correlative models are calibrated with existing data. Therefore it is impossible to model unexpected effects which never happened in the past. Yet there is an urgent need from the stakeholders to identify early tipping points as proxy of regime shifts to avoid crisis before its emergence ([Zimmermann et al., 2009](#)).

Mathematical bioeconomic models offer promising answers to these two limits. First the approach is less dependant to datasets and softwares. Second the modeling of the explicit processes makes possible the integration of events out of the set of calibration, including crisis effects. In this context, we understand that bioeconomic models offer a complementary tool to the popular correlative models. Actually, a variety of modelling approaches may often be available for addressing the social-ecological system research questions. As mentioned by the IPBES report ([IPBES, 2016](#)), debates about the use of correlative versus process-based models are frequently polluted by misconceptions about the utility of these models. Yet, many modelling exercises have clearly illustrated the benefits of combining multiple model types since it improves the quality of the management of social-ecological systems by providing complementary understandings of the research question and limitating uncertainty ([Cheaib et al., 2012; Gritti et al., 2013; van Oijen et al., 2013](#)).

Due to this complementarity, we support that the ongoing decline of the mathematical bioeconomic method is not desirable and merits to be reverse. This reversal calls therefore for improvements in adequacy between the method and the social demand from decision-makers.

### 3 Challenges for bioeconomic models

Our methodological cartography makes possible to observe that bioeconomic models have gradually improved over time. First, we highlighted the evolution of the model features in both paradigms. While earlier models lacked an inclusion of uncertainty, whether through a stochastic component in the ecological or economic model or a sensitivity analysis on the model parameters, they gradually evolved to take into account several forms of uncertainty, for example in the form of stochastic population dynamics ([Bulte and Kooten, 1999](#)) or uncertainties in the value of ecosystem services ([Augeraud-Véron et al., 2019](#)). However, in line with [Drechsler \(2020\)](#), it appears that uncertainty remains to be systematically integrated and considered as a major modeling component.

Second, the bioeconomic method has gradually encompassed the spatial dimension, and recognized its importance in both model components. Following [Sanchirico and Wilen \(1999\)](#), the spatial component has been integrated on the ecological side, in the form of a "patchy resource", paving the way for spatially differentiated population dynamics, namely meta-populations. The use of spatially differentiated data for ecological processes, including different habitat qualities, has gradually increased as well as spatially differentiated economic components. Third, a variety of actors have been gradually included, ranging from a single resource owner to complex property rights settings (local conservation agencies and communities competing for the resource ([Skonhoft, 1998](#)) , neighboring farmers facing a common threat of invasive species ([Fenichel et al., 2014](#))) and political settings (with the integrated management, by a social planner, of heterogeneous farmers ([Mouysset et al., 2014](#)) through public policies). Eventually, the process-based models we reviewed have gradually included some key components of correlative-methods, in order to be applied to real world settings and to provide policy guidance and evaluation. For example, species-area relationships have gradually been included. Notably [Davis et al. \(2006\)](#) investigate efficient conservation measures in a utility maximizing framework, where they used a species-area relationship to measure the value of conservation in the Sierra Nevada bioregion of California, instead of designing a fully tractable species model. These different improvements testify ways to better fit real-world conditions and thus answer to social expectations from decision-makers managing concrete terrestrial social-ecological systems.

However these improvements do not totally overcome the challenges. For example, explicit geographic economic components remain mostly absent from our sample and constitute an on-going challenge of bioeconomic models. Likewise, the articulation of actors within social-ecological systems remains an unsolved question since a wider variety of actors, especially local stakeholders and house-

holds, could better be taken into account.

Beyond these methodological examples in direct lines with our cartography, we can point out some more general fruitful avenues for future methodological improvements of bioeconomic models to better fit with stakeholders' needs. First, regarding the human-nature paradigm: indigenous standpoints and different value cultural systems should more systematically integrate into bioeconomic models which remain for now grounded in Western-Occidental ethics ([Kneese and Schulze, 1985](#)). Especially, spirituality underpinning the value of nature could be integrated, although existing works such as [Lopes and Atallah \(2020\)](#) investigate trade-offs and perform valuations of spirituality based on the framework pioneered by [Krutilla \(1967\)](#). Second, regarding the methodology : a more systematic use of statistical approaches developed by correlative models to calibrate or interpret the process-based modeling might provide the in-real anchorage desired by decision-makers. Third, regarding the communication platform. Inspired by correlative models, it would probably be strategic to provide easy-to-use softwares which generate the results of simulations pending on a set of parameters that the user can change. Even if the results can be expressed in stylized facts, this way of communication is not operational for practitioners.

## 4 Technical limitations and perspectives

Our cartography relies on a review which might be discussed at several levels. First of all, in spite of our efforts, we could not access *Forest Science*, a leading review in forestry. Therefore, forestry is underepresented in our sample. That being said, a sizeable share (16%) of our sample focuses on the topic. Second, our review procedure encompasses several criteria with a high level of generality. This methodological choice aims at filling a gap in the literature since most of the reviews focus on a smaller level. However, refining our methodological criteria, such as the ecological models we considered (population dynamics v. others) or the framing of uncertainty (absent or present, it can be refined through an analysis of stochasticity, sensitivity analysis) might help to precise the groups depicted by the MCA and thus help to connect our cartography to existing reviews, such as [Eppink and van den Bergh \(2007\)](#) and [Castro et al. \(2018\)](#). Third, our methodological characterization relies on a K-modes algorithm, an extension of K-means. Although well performing, the potential of such algorithms is limited by the number of observations. Given the number of variables and potential values, our sample size could limit the power of the K-modes algorithm in retrieving the structure of the dataset. In this perspective, other classification algorithms merit investigation to assess the robustness of our cartography. Fourth, our narrative elicitation with text data can be viewed as coarse, given that it only

encompasses word counts and lexical groups. Further analysis should deploy a more comprehensive method to analyze narratives quantitatively, and select a limited sample to conduct in depth analysis of narrative structures. Moreover other semantic fields might be investigated to precise the narrative underlying the different groups.

Finally, we adopted here a method perspective to cartography the bioeconomic models. We complete this perspective with some sociological information related to geographical origins of the researchers and to disciplines in which articles are published. However at this stage this information remains scarce and merits to be deepened by a specific sociological analysis. For example, connections between labs and institutions as well as between researchers measured by professional relationships (PhD student & supervisor), and citation networks such as in [Smessaert et al. \(2020\)](#) could yield interesting results. Regarding disciplinary aspects, an epistemological discussion would constitute a valuable addition in this economic field at the interface with natural sciences. All these elements might be used to precise our cartography but might also be the basis of new cartographies which could be confronted to the methodological ones. Convergences or divergences between technical, sociological and epistemological stakes might be this way highlighted.

## Acknowledgements

We are thankful to two anonymous referees and the editors for their valuable suggestions and comments.

## Appendix

### E Article selection equation on SCOPUS

In order to select articles, we performed a research on SCOPUS using the following query :

TITLE-ABS-KEY ( biodiversity AND ( ecological-economic OR bio-economic OR economic ) AND modeling ) AND ( LIMIT-TO ( SUBJAREA , "ENVI" ) OR LIMIT-TO ( SUBJAREA , "AGRI" ) OR LIMIT-TO ( SUBJAREA , "SOCI" ) OR LIMIT-TO ( SUBJAREA , "EART" ) OR LIMIT-TO ( SUBJAREA , "ECON" ) OR LIMIT-TO ( SUBJAREA , "ENER" ) OR LIMIT-TO ( SUBJAREA , "ENGI" ) OR LIMIT-TO ( SUBJAREA , "COMP" ) OR LIMIT-TO ( SUBJAREA , "MATH" ) OR LIMIT-TO ( SUBJAREA , "DECI" ) OR LIMIT-TO ( SUBJAREA , "BIOC" ) OR LIMIT-TO ( SUBJAREA , "MULT" ) OR LIMIT-TO ( SUBJAREA , "BUSI" ) OR LIMIT-TO ( SUBJAREA , "ARTS" ) )

TITLE-ABS-KEY (bioeconomic AND modeling) LIMIT-TO ( SUBJAREA , "ENVI" ) OR LIMIT-TO ( SUBJAREA , "AGRI" ) OR LIMIT-TO ( SUBJAREA , "SOCI" ) OR LIMIT-TO ( SUBJAREA , "EART" ) OR LIMIT-TO ( SUBJAREA , "ECON" ) OR LIMIT-TO ( SUBJAREA , "ENER" ) OR LIMIT-TO ( SUBJAREA , "ENGI" ) OR LIMIT-TO ( SUBJAREA , "COMP" ) OR LIMIT-TO ( SUBJAREA , "MATH" ) OR LIMIT-TO ( SUBJAREA , "DECI" ) OR LIMIT-TO ( SUBJAREA , "BIOC" ) OR LIMIT-TO ( SUBJAREA , "MULT" ) OR LIMIT-TO ( SUBJAREA , "BUSI" ) OR LIMIT-TO ( SUBJAREA , "ARTS" ) )

TITLE-ABS-KEY (bioeconomic AND model) LIMIT-TO ( SUBJAREA , "ENVI" ) OR LIMIT-TO ( SUBJAREA , "AGRI" ) OR LIMIT-TO ( SUBJAREA , "SOCI" ) OR LIMIT-TO ( SUBJAREA , "EART" ) OR LIMIT-TO ( SUBJAREA , "ECON" ) OR LIMIT-TO ( SUBJAREA , "ENER" ) OR LIMIT-TO ( SUBJAREA , "ENGI" ) OR LIMIT-TO ( SUBJAREA , "COMP" ) OR LIMIT-TO ( SUBJAREA , "MATH" ) OR LIMIT-TO ( SUBJAREA , "DECI" ) OR LIMIT-TO ( SUBJAREA , "BIOC" ) OR LIMIT-TO ( SUBJAREA , "MULT" ) OR LIMIT-TO ( SUBJAREA , "BUSI" ) OR LIMIT-TO ( SUBJAREA , "ARTS" ) )

### F Lexical groups

**Agriculture :** agriculture, agricultural, crop, rangeland, livestock, forage, fallow, farmland, grassland, oats, agri, farmers, grazing, crop, livestock, farming, wheat, crops, farm, cropping, rangeland, grazing, stocking, alfalfa, wheat, agro, crofting,

pastures, ranchers, range, grasslands

**Forest :** Trees, stand, tree, forest, forestry, basal, spruce, even-aged, uneven-aged, forests, timber, diameter, wood, pine, faustmann, volume, reforestation, rotation, rotational, acacia, forested, lichen

**Invasive species :** Invasive species, invasive, rabies, invasion, invasivespecies, invader, coevolution, non-endemic, nis, eradication, pest, mountainpinebeetle, weevil, disease, gypsymoth, weevil, oats, weed, herbicide, invader, rabies, pathogens, invasivespecies, indigenous, barrier, infestation, alien, beaver, calvescens, eradicate, host, resistance, infestations, pesticide, pests, invasions, weed, weeds , pest, nonindigenous, pathogen, invaders, spartinaalterniflora, spartina, beetle, endemic, emeraldashborer, beetles, avena, rodent, serratedtussock, tuberculosis, miconiacalvescens, vaccine, insects, spread, vector-borne, epidemiology, quarantine, trap

**Endangered/remarkable species :** Endangered species, remarkable, trophy, tiger, endangeredspecies, warbler, moose, illegal, threatened, threats, endangered, elephants, butterfly, wildlife, game, poachers, wolf, reindeer, poaching, wolves, elephant, bushmeat, ivory, black, hunt, canislupus, hunters, bear, serengeti, tigers, deer, rhino, extinction, endangered

**Policy :** Policy, subsidy, tax, tradable, subsidies, instruments, policy, policies, payments, taxes, market, markets, incentives, payment, permits, taxes, incentive, funding, budget, budgets, conflict, conflicts, bonus, planner, taxation, property, market-based, contracts, interventions, intervention, strategy, propertyrights, tax-subsidy

**Risk :** risk, uncertainty, insurance, markov, option, resilience, stochastic, probabilities, uncertain

**Conservation :** conservation, park, reserve, sites, restoration, planning, conservationplanning

**Harvesting :** harvesting, harvests, harvest, hunting

## G Supplementary tables

	<i>Biodiversity measure</i>	<i>Proxy measure</i>	<i>Biodiversity state variable</i>
<b>Biodiversity characterization</b>	Per se Proxy	No - per se Habitat Economic activity Conservation budget Not specified	Population Species Community (species & population) Not specified
	<i>Biological diversity</i>	<i>Biodiversity contribution level</i>	
	Functional Genetic Functional & genetic	Single species Multiple species Unknown	
<b>Ecological specifications</b>	<i>Dynamics</i>	<i>Spatiality</i>	<i>Uncertainty</i>
	Pop. dyn. Other	Explicit Implicit Absent	Stochastic Deterministic
<b>Bioeconomic linkage specifications</b>	<i>Biodiversity monetarization</i>	<i>Bioeconomic problem</i>	<i>Biodiversity stake</i>
	Yes No	Cost-benefit analysis Cost-effectiveness analysis	Constraint Objective Other
<b>Economic specifications</b>	<i>Dynamics</i>	<i>Spatiality</i>	<i>Uncertainty</i>
	Static Dynamic	Explicit Implicit Absent	Stochastic Deterministic
<b>General characteristics</b>	<i>Solving method</i>	<i>Data anchorage</i>	<i>Model use</i>
	Closed form Numerical solution Both	Theoretical Empirical Both	Normative Descriptive
	<i>Equilibrium</i>		
	General Partial		

Table 1.A: List of the methodological criteria and their related items used to perform the methodology-based cartography. In grey stand the criteria which have been excluded after the sensitivity analysis of the MCA.

<i>Economic journals</i>	<i>Count(60%)</i>	<i>Ecology journals</i>	<i>Count(26%)</i>
Ecological Economics	44	Ecological Modelling	15
American Journal of Agricultural Economics	19	Biological Conservation	11
Journal of Environmental Economics and Management	19	Ecological Applications	11
Environmental and Resource Economics	15	Canadian Journal of Forest Research	6
Resource and Energy Economics	15	Journal of Applied Ecology	6
Land Economics	11	Conservation Biology	4
Environment and Development Economics	6	Forest Science	4
Journal of Bioeconomics	6	Diversity and Distributions	3
Journal of Environmental Management	6	Forest Ecology and Management	3
Agricultural Economics	4	Biological Invasions	2
Review of Agricultural Economics	4	Conservation Letters	2
Australian Journal of Agricultural Economics	3	Ecology Letters	2
Journal of Economics	3	Biodiversity and Conservation	1
Journal of Forest Economics	3	Commonwealth Forestry Research	1
Agricultural and Resource Economics Review	2	Ecological Indicators	1
American Economic Review	2	Ecology and Society	1
European Review of Agricultural Economics	2	Environmental Entomology	1
Journal of Economic Theory	2	European Journal of Forest Research	1
Canadian Journal of Economics	1	Journal for Nature Conservation	1
Computational Economics	1	Journal of Economic Entomology	1
Econometrica	1	Journal of Forestry Research	1
Economic Inquiry	1	Journal of Theoretical Biology	1
Economic Theory	1	New Forests	1
Journal of African Economies	1	Silva Fennica	1
Journal of Agricultural and Applied Economics	1	Theoretical Population Biology	1
Journal of Agricultural and Resource Economics	1	Wildlife Biology	1
Journal of Agricultural Economics	1		
Journal of Economic Dynamics & Control	1		
Kiel Working Papers	1	<i>Sustainability science journals</i>	<i>Count (10%)</i>
Management Science	1	Natural Resource Modeling	10
MPRA Papers	1	Agricultural Systems	3
MPRA Working Papers	1	Environmental Modeling and Software	2
Oxford Economic Papers	1	Environmental Modeling and Assessment	2
Review of marketing and Agricultural Economics	1	PNAS	2
RFF Discussion papers	1	Australian Journal of Experimental Agriculture	1
Social Choice and Welfare	1	Central European Journal of Operations Research	1
Socio-Economic Planning Sciences	1	Climatic Change	1
Spatial Economic Analysis	1	EcoHealth	1
The Australian Journal of Agricultural and Resource Economics	1	Ecosystem Services	1
The B.E. Journal of Economic Analysis and Policy	1	Journal of Biological Dynamics	1
The Journal of Political Economy	1	Journal of Environment Management	1
Western Journal of Agricultural Economics	1	Land Use Policy	1
		Nature	1
<i>Applied Mathematics journals</i>	<i>Count (4%)</i>	Non Linear Analysis	1
Journal of Mathematical Analysis and Applications	2	Operations Research	1
Journal of Mathematical Biology	2	PLoS One	1
Applied Mathematics Letters	1	Proceedings of the Royal Society	1
Biometrics	1	Regional Environmental Change	1
Bulletin of Mathematical Biology	1	Science	1
Computers and Mathematics with Applications	1		
Journal of Optimisation Theory and Applications	1		
Mathematical Biosciences	1		
Mathematical Biosciences and Engineering	1		
Mathematical Models and Methods in Applied Science	1		

Table 1.B: Journal distributions among disciplines

## H Supplementary figures

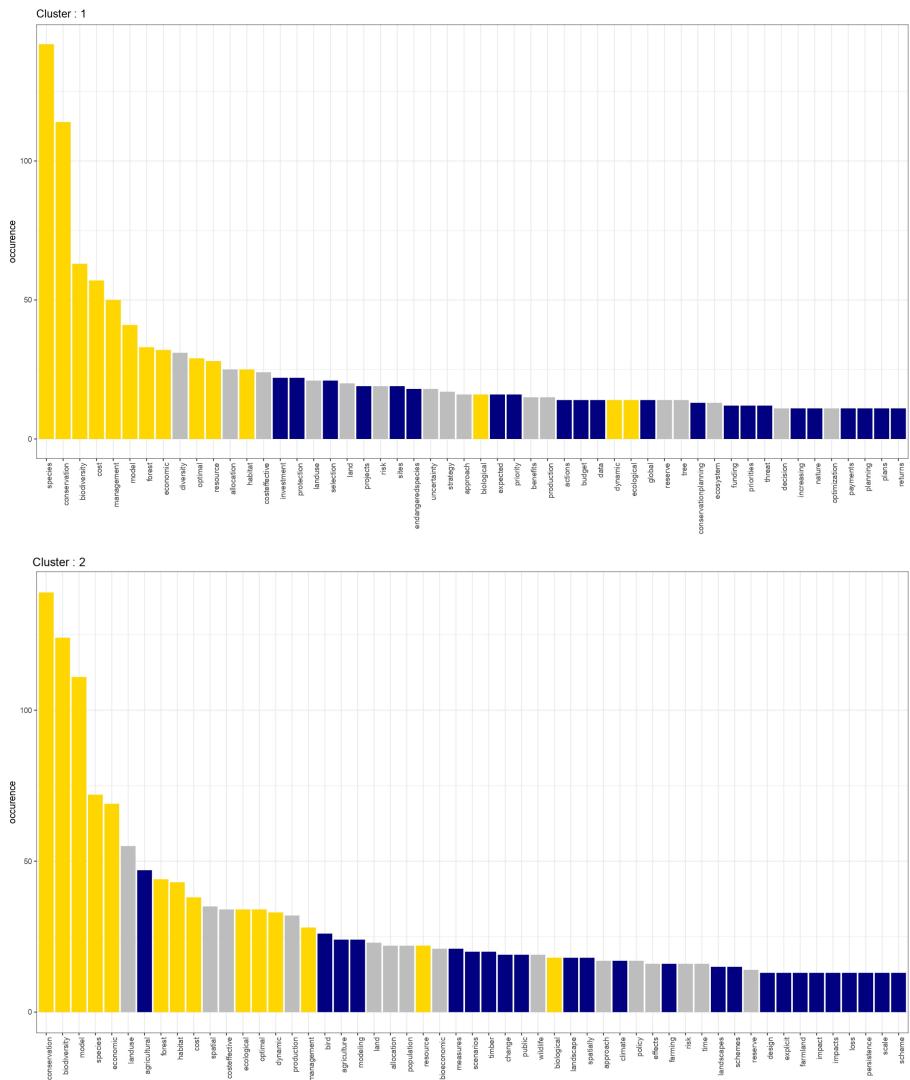


Figure 1.A: Distribution profiles of the 50 words the more frequent for methodology-based groups 1 and 2

In yellow stand the words in common among the 4 profiles. On the opposite in blue stand the words specific to a profile

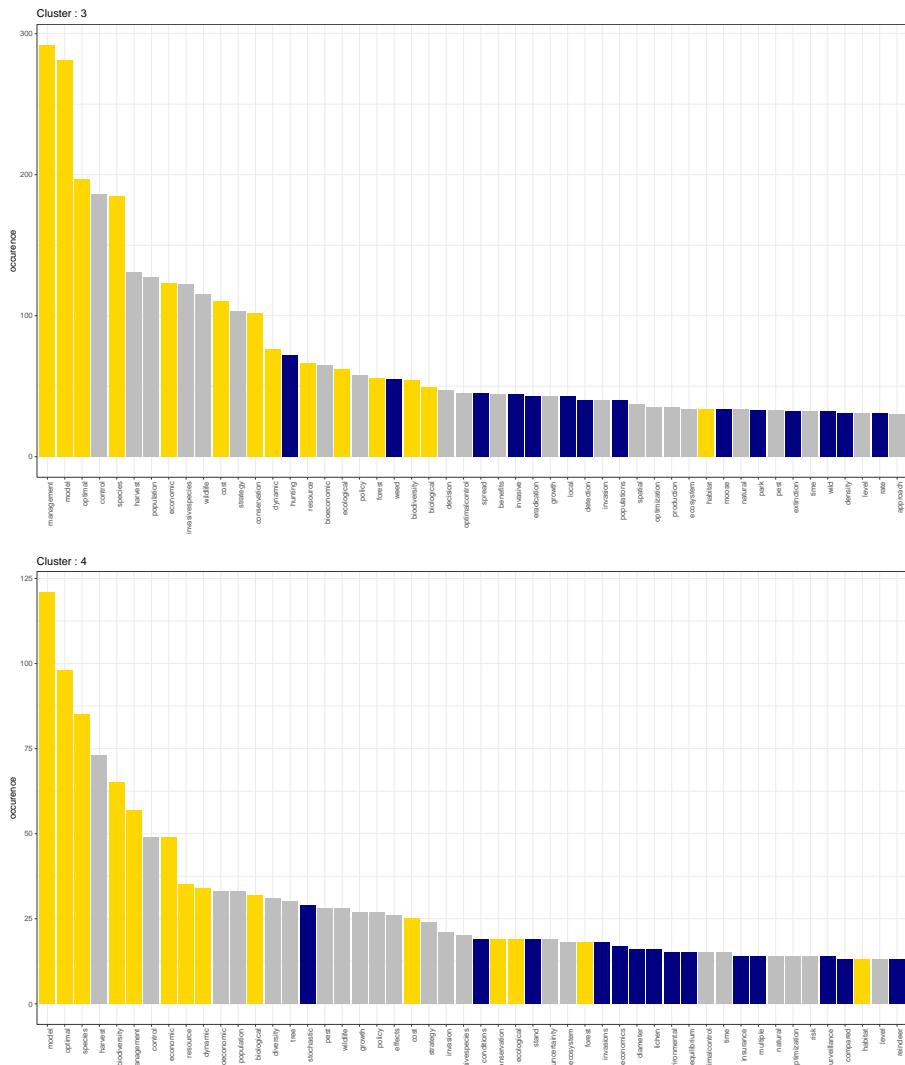


Figure 1.B: Distribution profiles of the 50 words the more frequent for methodology-based groups 3 and 4

In yellow stand the words in common among the 4 profiles. On the opposite in blue stand the words specific to a profile

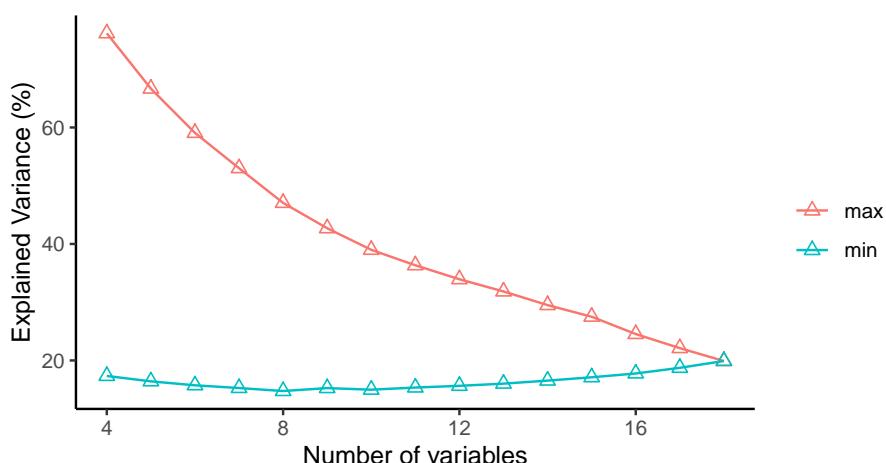


Figure 1.C: Explained variance function of the number of methodological criteria used in the MCA.

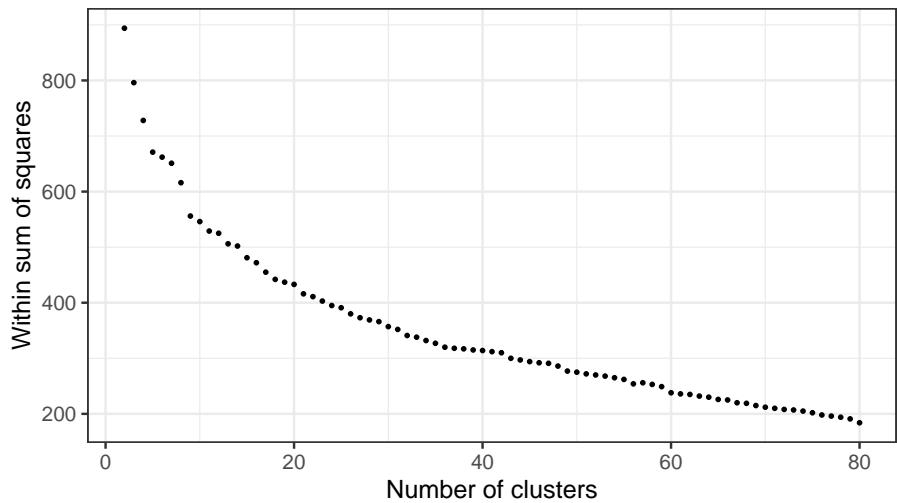


Figure 1.D: Cost function of the K-modes.

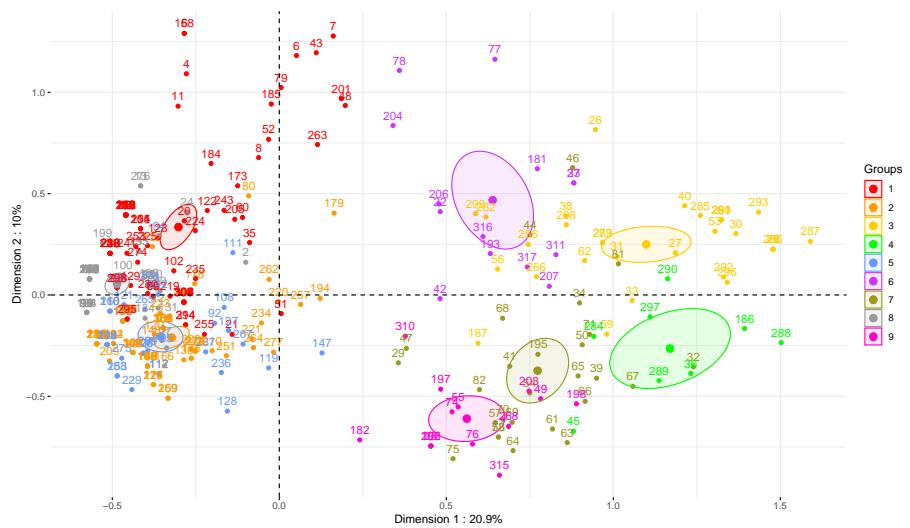


Figure 1.E: Multiple Correspondence Analysis (MCA) running on 12 methodological criteria and 9 groups.

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# Chapter 2

## The wildfire-habitat connectivity dilemma: a graph theoretical approach to landscape management

Background: Fuel treatment operations help to mitigate the spread and severity of wildfires in numerous ecosystems. As they aim at fragmenting the fire landscape, they also fragment wildlife posing a dilemma for land managers. We use graph theory on simulated to gain a general understanding of the allocation of treatments over space and time and the corresponding landscape properties with various habitat connectivity targets.

Results: Our results show that all initial landscapes converge to steady-state landscape cycles. Optimal trajectories significantly reduce wildfire risk while safeguarding habitat connectivity. As the policy budget increases, more risk reduction is achieved, albeit with a decreasing marginal efficiency. As habitat targets increase, increasing the budget is of no effect, and risk increases. Landscapes are less risky, more fragmented, and diverse when the budget is large and biodiversity targets are low, while they are more compact and less diverse when the opposite is true. Treatment allocation follows graph centrality measures, and central cells are treated first. When biodiversity targets increase, central cells are no longer treated as they decrease habitat connectivity. Treatment is reshuffled to the edges of the landscape.

Conclusion: Computational experiments generalize existing results. Using graph theory, general insights can be gained, and help managers faced with multiple objectives in forested landscapes. From a policy perspective, in the face of climate change, increasing treatment budgets should be a priority to avoid increasing damages. A key guideline is treating *adolescent* successional stages and fragment *mature* patches to mitigate risk and guarantee the connectivity of wildlife habitat in small scale landscapes, but small scale results do not scale up to large landscapes.

Keywords : Fuel treatment, connectivity, wildfire risk, wildlife habitat, spatial optimization, graph theory

JEL codes : Q57, Q23, Q54, C63

# 1 Introduction

Hazardous and intense wildfires destroy forest cover<sup>1</sup>, threaten forest resilience and can cause ecosystem shifts, ranging from changes in forest structure to changes towards non-forest ecosystems (Coop et al., 2020). Additionally, intense wildfires cause human damages, in the form of direct asset losses: in 2018, wildfires in California have caused \$ 27 billion (Wang et al., 2021). Indirect costs are also of concern, especially related to wildfire smoke : increases in PM 2.5 concentrations have important health impacts (Burke et al., 2023; Heft-Neal et al., 2023), smoke directly affects recreation values in the US, amounting to \$USD 2.3 billion in welfare losses (Gellman et al., 2024). Aside from directly measurable costs, wildfires also cause dramatic impacts on biodiversity across taxa (Wintle et al., 2020), through direct population losses and durable habitat disruption (Ayars et al., 2023).

In a business as usual scenario in terms of forest management, wildland-urban interface expansion and climate change, these direct and indirect costs and damages to both humans and non-humans are expected to increase drastically. Decades of wildfire suppression have created a “wildfire deficit”, which increases the probability, extent and severity of wildfires in the western United States (Kreider et al., 2024). European forests are not adapted to climate change induced wildfire risks (Khabarov et al., 2014), in terms of species composition and use of fuel management operations. Mechanical thinning, prescribed burns, and sometimes, logging, have been leveraged to decrease the fuel load in risky areas and theoretically decrease the probability and severity of burns upon wildfire occurrence<sup>2</sup>. In numerous regions, such as conifer forests in California (Vaillant et al., 2009; Kalies and Yocom Kent, 2016; Low et al., 2023), eucalypt forests in South Western Australia (Burrows and McCaw, 2013; Boer et al., 2009; Florec et al., 2020), southern Europe (Fernandes et al., 2013), evidence shows that fuel treatments, can mitigate wildfire intensity and spread. Land management agencies have historically implemented these policies in Australia (Burrows and McCaw, 2013), Europe, and the United States (and are projected to ramp up, for example under the Infrastructure Investment and Jobs Act of 2021 in the US). While potentially useful, the use of these treatments is still hindered by numerous obstacles (Miller et al., 2020) and remains insufficient<sup>3</sup>. Additionally, the extension

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<sup>1</sup>From 2001 to 2023, forest loss attributed to wildfires amounted to 138 million hectares (roughly 33% of the surface of the European Union) (Tyukavina et al., 2022)

<sup>2</sup>The efficiency of these measures depends on environmental and terrain variables. For example, prescribed burns are efficient every 1-4 years in reducing risk and severity only in the case of non-extreme weather conditions, and when the terrain ruggedness is limited (Bradstock et al., 1998)

<sup>3</sup>However, recent bills have been passed in the US (Infrastructure Investment and Jobs Act of 2021) and California to ramp up the use of prescribed burns - such as the bugdget act of 2022,

of wildland-urban interfaces (WUI) increases the extent of potential damages as well as ignition probabilities (Radeloff et al., 2018).

As global warming affects water supply and fuel moisture (Jolly et al., 2015; Abatzoglou and Williams, 2016; Ruffault et al., 2018), it is projected to increase the frequency, severity, and magnitude of wildfires (Dupuy et al., 2019; Wasserman and Mueller, 2023). Recent wildfire events in California (since 2018), in Australia (2019-2020), and in Europe (France, Portugal, Greece in 2022) have epitomized these trends. Moreover, wildfires and climate change are endogeneously linked in a positive feedback loop : large wildfires are of importance in the face of climate change; as they release large amounts of greenhouse gases (1.7GtC per year on average between 2003 and 2022) and reduce the extent of terrestrial carbon sinks (Zheng et al., 2023; Friedlingstein et al., 2023; Byrne et al., 2024).

In the face of a growing threat to human assets and biological diversity, increasing the efficiency of fuel treatments to manage multiple objectives is paramount. A decision framework that accounts for wildfire processes and biological diversity drivers is paramount to deliver policy recommendations that simultaneously achieve wildfire damage reduction and protect biological diversity (Driscoll et al., 2010). Among the decision levers, the extent and location of treatments are key variables.

By changing the structure of the landscape, fuel management operations may reduce the risk and associated damages of wildfires. Treatments achieve larger risk reduction when located close to the values at risk instead of being dispersed across the landscape (Ager et al., 2007; Williams et al., 2017; Florec et al., 2020). However, they also affect the structure of biodiversity habitat, notably, its structural connectivity (Taylor et al., 1993). Maintaining habitat connectivity, through wildlife corridors, landscape links, and ecoducts (Turner, 2005; Turner and Gardner, 2015), is instrumental in mitigating the biodiversity crisis. Species richness and diversity are intimately linked to landscape connectivity (Olds et al., 2012; Tian et al., 2017; Velázquez et al., 2019) and are necessary to maintain ecosystems in the future. Fragmentation, conditional on habitat surface being constant, may enhance biodiversity (Tischendorf and Fahrig, 2000; Hu et al., 2012; May et al., 2019). However, it is often accompanied with habitat loss, detrimental to biodiversity (Fahrig, 2003). The use of fuel management operations alters the structure of the landscape e.g. both habitat and matrix<sup>4</sup>, in terms of temporal and spatial variation in landscape configuration and composition. As habitat is altered, so is the surrounding matrix, which can impede species movement (Eycott et al., 2012; Kuefler et al., 2010) and alter evolution and selective regimes (Cheptou et al.,

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committing \$2.8 billion to the Governor's Wildfire and Forest Resilience Action Plan - and limiting liabilities in the case of wildfire escape (see California Senate Bill SB-332) on private land.

<sup>4</sup>e.g. land use or cover, or environmental conditions that differ from eitehr species' habitat or reference natural conditions (Fletcher et al., 2024)

2017).

The impact of fuel treatments on biodiversity remains a debated topic. Evidence suggests that maintaining a variety of vegetation types and ages on a patchy landscape maintains a 'fire mosaic' (Sitters et al., 2015) (e.g. landscape level variations in habitat types that provide habitat to an ecological community) or that fuel treatment can be beneficial to wildlife (Saab et al., 2022; Loeb and Blakey, 2021) and even restore local populations (Templeton et al., 2011). On the other hand, treating at too high a frequency may be detrimental to biodiversity (Bradshaw et al., 2018), as vegetation with extensive juvenile period may disappear, and fauna that rely on them as well<sup>5</sup>, or high frequency treatment favors the invasion of fire tolerant, fire-enhanced weed species (van Wilgen, 2013).

Hence, fragmenting the wildfire risk poses significant threats to biodiversity in forest landscapes. Nonetheless, there may exist a range of spatial allocation patterns that take into account the location of protected species and can reduce threats to both assets and biodiversity (Ager et al., 2007; King et al., 2008; Rachmawati et al., 2018).

Eventually, wildfire risk and potential damages pose a significant challenge in terms of policy-making. As wildfire risks and potential damages are spatially heterogeneous, and as wildfires spread, they create a large spatial externality. Indeed, individual risk reduction (e.g. self-protection) is hampered by the influence of neighbors on individual risk, which results in the under provision of risk reduction (Shafran, 2008; Costello et al., 2017). Additionally, in a risky (e.g. stochastic) context, risk aversion may further reduce self-protection this phenomenon when financial insurance is limited (Ehrlich and Becker, 1972)<sup>6</sup>. Finally, the magnitude of potential damages (Costello et al., 2017) as well as the large information requirements for efficient fuel treatment planning warrant a collective approach.

In this context, we study the spatial patterns of treatment allocation that diminish potential damages from wildfires in where fire spread is governed by patch connectivity, while safeguarding biodiversity habitat connectivity, from a central decision maker perspective.

A substantial literature has applied optimization techniques to tackle the spatial allocation of fuel treatments. Analytical (Finney, 2001), simulation-based (Finney, 2007; Rytwinski and Crowe, 2010) or mixed-integer programming techniques (Wei et al., 2008) have solved the allocation of treatments in a static framework. Given the dynamic nature of fuel growth, studies based on mixed-integer dynamic programming (Wei et al., 2008; Minas et al., 2014; Rachmawati et al.,

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<sup>5</sup>For example, in Australia, species such as *Banksia baueri*, *B. nutans* and *B. baxteri* would disappear, threatening tammar wallabies, quokas and honey possums (Bradshaw et al., 2018)

<sup>6</sup>This is particularly the case in California, where repeated fire episodes have pushed insurers to spike contract premiums, or to not renew contracts- non renewal rates went from 11% in 2018 to 13% in 2021

2015, 2016) have studied the temporal and spatial allocation of fuel treatments on real and simulated landscapes. While they solve the spatial treatment allocation problem in forests, these articles fail to acknowledge the multiple uses and objectives land planners have to consider, such as habitat conservation. Several articles have devoted their attention to the spatial allocation of treatments while conserving habitat, and investigated the trade-offs between risk reduction and biodiversity conservation, using spatial heuristics (Calkin et al., 2005; Lehmkuhl et al., 2007) and linear programming (Williams et al., 2017; Rachmawati et al., 2018).

Most of the existing literature focuses on case studies and lacks a general interpretative framework to generalize its results. Graph theory offers a toolbox suited to analyze the properties of connected cells or patches of land with varying characteristics, and has extensively been applied in landscape ecology (Urban and Keitt, 2001; Minor and Urban, 2008; Rayfield et al., 2016). Conrad et al. (2012) and Jafari and Hearne (2013) use a specific graph theory algorithm - a network-flow model - to find the optimal subgraph of corridors connecting habitat areas. Their approach optimally connects patches of habitat spread across the landscape for a given species, in a reserve-network design problem fashion. Our approach adopts a more holistic perspective, as it emphasises the degree of connectedness between habitat cells, thus allowing for a multi-species and multi-scale perspective, instead of a corridor for a single species.

Recent research focusing on the allocation of fuel treatments has leveraged tools from graph theory (Matsypura et al., 2018; Pais et al., 2021a). Reconciling habitat and wildfire risk mitigation using graph theory is a recent research endeavor (Rachmawati et al., 2018; Yemshanov et al., 2022) and has focused on specific case studies.

In this article, we focus on the dynamic and spatial dimensions of the problem (thus abstracting from the stochastic components) and leverage graph theory to study the general patterns of treatment allocation emerging from a multi-objective, dynamic, and integer landscape management problem, governed by connectivity.

To do so, we first compare the optimal allocation of treatments using repeated static optimization and heuristic dynamic programming on a 5 period horizon on representative subsamples of small scale landscapes with an exhaustive range of habitat connectivity constraint. We show that for realistic biodiversity habitat constraint levels, the constraint imposed on the evolution of the forest results in similar structures for repeated myopic and dynamic optimization. Therefore, we analyse the treatment allocation and landscape structures emerging in the long run using repeated myopic optimization for all the possible initial landscape con-

figurations, in a graph theoretical framework. We explicit the trade-off between risk reduction and biodiversity habitat, in the form of a production possibility frontier (PPF). We characterize the landscapes using a range of ecological indicators and find general mechanisms and guiding principles applicable to a broad class of settings, to guide decision-makers and foster new efficient multi-objective graph theory algorithms. Finally, we test our predictions from a small scale landscape to simulated realistic large scale landscapes (10,000 cells) with varying composition and spatial autocorrelation, and compare them with different intuitive policy recommendations.

Our contributions are several. First, we provide a spatial framework to understand the trade-offs between wildfire risk reduction and biodiversity conservation. Second, we leverage the constraints imposed on a dynamic spatial system to show that repeated optimization performs relatively well compared to dynamic programming. Third, using graph theory, we derive general principles regarding the spatial characteristics of landscapes and treatments from an exhaustive set of theoretical landscapes to guide policymakers as well as future research in heuristics to reconcile conflicting land-based phenomenons.

## 2 Methods

### 1 Model description

We consider landscapes represented by a regular grid of  $n \times n$  standardized area cells in period  $t$  by  $\mathbf{A}_t$  with a forest seral stage succession module. Each cell  $a_{ijt} \in \mathbf{A}_t$  with  $\{i, j\} \in \{1, \dots, n\}^2$ , at time  $t$  is characterized by a successional stage: *juvenile*, *adolescent*, or *mature*, which translates into 3 numerical age classes ranging from 0 to 2. Each transitional seral stage has the same duration<sup>7</sup>, hence at each time step, it changes stage until it is in the *mature* stage, where it remains (eq 2.1)

We use a stylized representation of the link between vegetation age, habitat, and wildfire risk (figure 2.1).

First, we assume a cell offers suitable wildlife habitat once it is *adolescent* (eq. 2.2). Second, a cell can turn at critical risk of wildfire during a normal hot season when its successional stage is *mature* (eq. 2.3). We assume an Olsen-type model of flammability, where age class is the main predictor of flammability (Olson, 1963; McCarthy et al., 2001; McColl-Gausden and Penman, 2019). A cell remains at

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<sup>7</sup>For example, in Australia, McColl-Gausden and Penman (2019) use quasi evenly spaced age classes for heathland, tall-mixed, foothills, forby and wet vegetation types (see table 1); on the other hand, in coniferous forests in Western US (Washington and Oregon), Thomas (1979) developed a successional stage description for wildlife habitat management, still used by the USDA. 40 year transitional classes can be made grouping *grass-forb*, *shrub-seedling* and *pole-sapling* together and *young*. *Maturity* is reached at 80 until 159 years old, where it mutates into *old-growth*

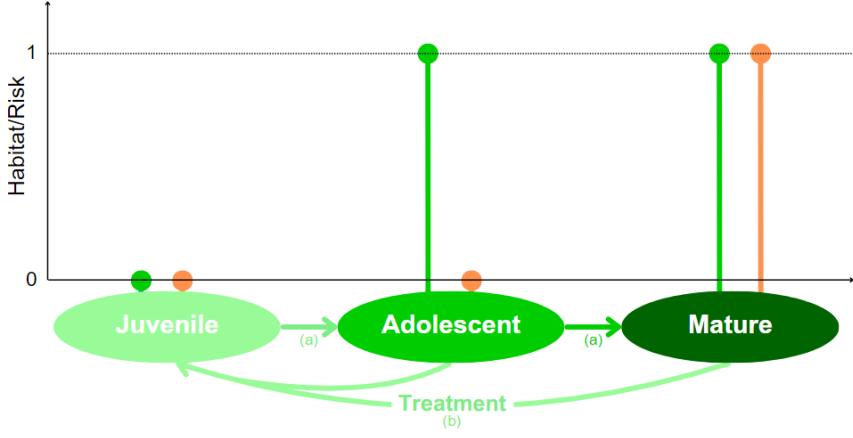


Figure 2.1: Illustration of the successional stages and the link between successional stage, habitat and wildfire risk using a discretized Olson-type relationship

At the bottom, the dynamics of the model are illustrated. First, successional stages transition (step (a)), then treatment is applied (step (b)). At the top, the link between successional stage, habitat and high risk. In green, a *habitat* variables turns to 1 when a cell is *adolescent*, and in orange, a *high risk* dummy turns to 1 when a cell turns *mature*

high risk as long as it is in the *mature* age class.

Finally, we consider fuel treatment to be a binary decision e.g. treatment is absent or present and there is no extensive margin, hence a treatment binary variable  $x_{ijt} \in \{0, 1\}$  represents the treatment status in cell  $a_{ij}$  a time  $t$ . The decision maker first observes the transition to the next successional stage, then decides upon treatment. Treatment can happen at any successional stage : whether at an *adolescent* stage, in anticipation of a cell becoming *mature* and turning at *high risk* in the next period, or as an immediate strategy upon becoming *mature* and thus, *high risk*. Upon treatment, a cell successional stage is reset to *juvenile* (eq. 2.1). Figure 2.1 illustrates the dynamics of the model.

Given a patch  $a_{ijt}$  and treatment status  $x_{ijt}$  in period  $t$ , equation 2.1 summarises the successional dynamics, and equations 2.4 and 2.3 summarize the link between successional stage, habitat, and high risk:  $\forall t, \forall \{i, j\} \in \{1, \dots, n\}^2$

$$a_{ijt+1} = \max((a_{ijt} + 1)(1 - x_{ijt}); 2) \quad (2.1)$$

$$\text{Habitat } (a_{ijt}) = \begin{cases} 1 & \text{if } a_{ijt} \geq 1 \\ 0 & \text{otherwise} \end{cases} \quad (2.2)$$

$$\text{Risk } (a_{ijt}) = \begin{cases} 1 & \text{if } a_{ijt} \geq 2 \\ 0 & \text{otherwise} \end{cases} \quad (2.3)$$

We use a network structure to apprehend the landscapes. From the matrix  $\mathbf{A}_t$ , we form two graphs:  $\mathcal{B}_t = (V_{\mathcal{B}_t}, E_{\mathcal{B}_t})$ , the graph of suitable habitat cells and

$\mathcal{F}_t = (V_{\mathcal{F}_t}, E_{\mathcal{F}_t})$ , the graph of high risk cells. First, the vertices of each graphs are the suitable habitat cells e.g  $V_{\mathcal{B}_t} = \{(i, j) \text{ such that } \text{Habitat}(a_{ijt}) = 1\}$  and the high risk cells, respectively e.g.  $V_{\mathcal{F}_t} = \{(i, j) \text{ such that } \text{Risk}(a_{ijt}) = 1\}$ .

Second, vertices are connected if they are within a Moore (or 8-cell) neighborhood of each other and share the same status. Therefore, notice that  $\mathcal{F}_t \subset \mathcal{B}_t$ . Figure 2.2 illustrate the mechanism from the landscape in matrix form  $\mathbf{A}_t$  with age classes ranging from 0 to 2, to graphs  $\mathcal{B}_t$  and  $\mathcal{F}_t$ .

We use this 8-cell neighborhood for evaluating biodiversity habitat and wild-fire risk within a common a spatial framework, using the same adjacency properties. Regarding biodiversity, we focus on general characteristics related to landscape structural connectivity rather than functional connectivity, as we are agnostic about effective species (Fahrig et al., 2011). We assume that species are able to disperse from one patch to another, and that habitat quality is uniformly distributed conditional on habitat being available.

We consider the wildfire risk through the lens of potential spread, influenced by fuel, wind direction and terrain. We abstract from wind patterns and terrain, to focus on fuel connectivity<sup>8</sup>. Consistent with the literature (see Peterson et al. (2009), Pais et al. (2021b); Gonzalez-Olabarria et al. (2023)), a wildfire can spread in any direction, conditional on neighbor cells with high risk.

To assess the connectivity of  $\mathcal{F}_t$  and  $\mathcal{B}_t$ , we use a global connectivity indicator. As connectivity can be measured in numerous ways in graph theory, we use this metric as it satisfies criteria pertaining to its evolution when vertices and edges are removed (Pascual-Hortal and Saura, 2006) when using graph theory applied to landscape ecology. Additionally, it offers a reformulation of the metric used in previous work closely related to ours (Minas et al., 2014; Rachmawati et al., 2016) (see appendix A for a demonstration). We define the global connectivity index of a given graph  $\mathcal{G} = (\mathcal{V}, \mathcal{E})$  as<sup>9</sup>:

$$H(\mathcal{G}) = \text{card}(\mathcal{V}) + 2\text{card}(\mathcal{E}) \quad (2.4)$$

Let a *patch* be a collection of connected cells of suitable wildlife habitat. This indicator considers that a habitat cell is connected to itself (i.e, within a habitat patch, there is no barrier) and whether it is connected to other cells. It implies lower connectivity when the distance between habitat cells increases, attains its maximum value when a single habitat patch covers the whole landscape, indicates lower connectivity as the habitat is progressively more fragmented, considers negative the loss of a connected or isolated cell, and detects as more important the loss of

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<sup>8</sup>Note that our framwork is amenable to prevailing wind patterns and terrain ruggedness, as the graph adjacency matrix can change from a Moore adjacency to any pattern influenced by environmental features

<sup>9</sup>With  $\text{card}$  being the cardinal operator in set theory and denotes the number of elements in a set

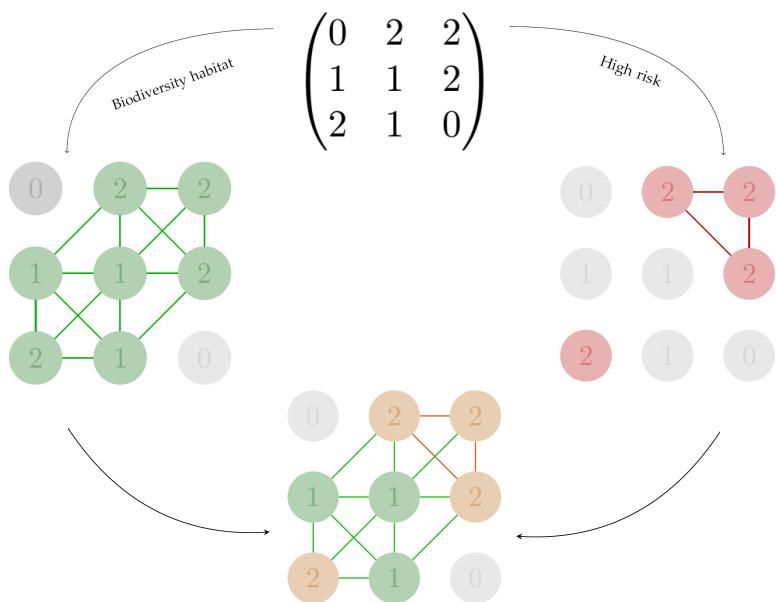


Figure 2.2: Illustration of the suitable habitat and high risk graphs for  $n = 3$

The first layer is the values from a raster  $\mathbf{A}_t$  of age classes in a forest landscape. It is turned into two different graphs.

In the left graph, the green vertices are  $V_{\mathcal{B}_t}$  and support biodiversity habitat, while on the right graph, red vertices are  $V_{\mathcal{F}_t}$  display high risk. Green and red links are respectively  $E_{\mathcal{B}_t}$  and  $E_{\mathcal{F}_t}$ . The high risk graph has two components (top right corner with 3 nodes, and bottom left corner with 1 node), while the biodiversity habitat graph only has one.

Cells for which the value is 0 are not considered as nodes for both graphs, and are thus not connected to the rest of the graphs.

In the final landscape, because  $\mathcal{F}_t \subset \mathcal{B}_t$ , the landscape where orange cells are high fuel load and also support biodiversity habitat (e.g.  $a_{ijt} \in V_{\mathcal{B}_t} \cap V_{\mathcal{F}_t}$ )

bigger patch, and less important steppingstone cells or patches.

Our global connectivity indicator is similar to the notion of *energy of a graph* (Gutman, 2001), which can be understood as a measure of connectedness (highly connected graphs tend to have high energy) for graphs. However, we differ from Gutman (2001) by including self-loops as habitat cells and patches are connected to themselves. Our formulation of  $H$  reframes a quadratic form from the adjacency matrix of a graph grid structure (appendix A). The adjacency matrix displays interaction among nodes that are neither purely constructive or destructive, as some combinations of active neighboring nodes will add to global connectivity, while other combinations may subtract global connectivity. In all the landscape sizes we used, eigenvalues of the adjacency matrix were both positive and negative, leading to indefiniteness (see figure 2.A). Therefore,  $H$  is not globally convex nor concave.

## 2 Social planner decision : the high-risk /connectivity dilemma

### 2.1 Dynamic decision problem

A social planner tries to minimize the global connectivity index of the high risk graph, using fuel treatments (eq. 2.5). However, when implementing treatment, a cell's successional stage is reset to *juvenile*, thus destroying biodiversity habitat. In coherence with real world applications, the social planner is faced with a temporal budget constraint (e.g. the sum of treatments  $\sum_{ij} x_{ijt}$  must be lower or equal to the *Budget* - eq. 2.9) as well as an ecological constraint, in terms of biodiversity habitat connectivity (e.g. the global connectivity of biodiversity habitat  $H(\mathcal{B}_t)$  must be larger than constraint *Biod* - eq. 2.7). Both the ecological and budget constraint need to be satisfied in each period.

For the sake of the analysis, we focus on two layers of complexity : time and space. We do not include a stochastic component related to wildfire risk e.g. we adopt a deterministic framework where the value at risk (global connectivity of risky cells) is weighed against the loss in biodiversity habitat connectivity. Additionally, we consider a homogeneous distribution of treatment costs across the landscape e.g. cost of treatment in each cell through time is 1. We come back to this assumption in the discussion. Monetary benefits are also homogenously distributed across the landscape, and normalized to 1. Note that there is, however, heterogeneous returns to treating across the landscape : some cells will contribute more than other to global connectivity. Finally, given that the planning horizon is finite, we do not discount future high risk connectivity scores and assume each period is equally important in decision making.

The optimization problem is :

$$\min_{\{\{x_{ijt}\}_{(i,j)}\}_{t=1}^T} \left[ \sum_{t=1}^T H(\mathcal{F}_t) \right] \quad (2.5)$$

Such that:

$$\mathbf{A}_0 \text{ given} \quad (2.6)$$

$$\forall t \in \{1, \dots, T\} :$$

$$H(\mathcal{B}_t) \geq Biod, \quad (2.7)$$

$$\text{and } \forall (i, j) \in \{1, \dots, n\} :$$

$$a_{ijt+1} = \min((a_{ijt+1}(1 - x_{ijt}); 2), \quad (2.8)$$

$$\sum_{i,j} x_{ijt} \leq Budget, \quad (2.9)$$

$$x_{ijt} \in \{0, 1\} \quad (2.10)$$

Notation	Concept
$\mathbf{A}_t$	Landscape matrix representing successional stage at time $t$
$a_{ijt}$	Cell $(i, j)$ of landscape with value $\in \{0, 1, 2\}$
$x_{ijt}$	Treatment status $\in \{0, 1\}$ of cell $(i, j)$ at time $t$
$H$	Global connectivity measure
$\mathcal{F}_t = (V_{\mathcal{F}_t}, E_{\mathcal{F}_t})$	Graph of high risk cells
$\mathcal{B}_t = (V_{\mathcal{B}_t}, E_{\mathcal{B}_t})$	Graph of suitable habit cells
$Biod \in \{0, \dots, \max H(\mathcal{B})\}$	Level of habitat global connectivity constraint
$Budget \in \{1, 2, 3, 4\}$	Level of the budget constraint
$n \in \{4, 100\}$	Size of the landscape
$c = 3$	Number of age classes
$T \in \{5, 10\}$	Planning horizon

Table 2.1: Summary of model variables and functions

As common in the literature, we can express the budget as a share of land being treated ranging from 5 to 25% of the surface area (when  $n = 4$ ). These values encompass historical and projected policies in Australia (Burrows and McCaw, 2013), the United States (Office, 2019) and Southern Europe (Fernandes et al., 2013).

Additionally, we solve the problem for a range of possible habitat connectivity values, ranging from 0 to the maximum possible habitat connectivity for each landscape size  $n$ .

## 2.2 Non-convexity and dimensionality curse

Our problem can be classified as a *critical node detection problem*, i.e, a problem of locating the vertices that best degrade connectivity, such that the number of components increase, and within remaining components, nodes with the largest *centrality* are targeted (Arulselvan et al., 2009). As definitions of *graph centrality* matter, we refine our approach in section 4.2. Problems of the critical node class are computationally difficult (e.g. NP - Hard) in a single graph (Arulselvan et al., 2009; Matsypura et al., 2018). Efficient heuristics to find near-optimal solutions exist and leverage perturbations around local solutions (Arulselvan et al., 2009; Zhou and Hao, 2017). Compared to the canonical *critical node detection* problem, our problem features a non-convex objective function, a budget constraint, and a constraint on habitat connectivity, which imposes a constraint on the supergraph of high risk cells. Given our constraints, the behavior of the global connectivity measure  $H$ , standard optimization techniques cannot be applied, and heuristics are required.

In dynamic problems, a standard technique is dynamic programming (Bellman, 1957). Dynamic programming provides a temporal decomposition of the initial problem defined over  $T$  periods, into  $T$  recursive problems, as it relies on the 'optimality principle'<sup>10</sup>. A value function  $V$ , mapping each possible state of the world e.g.  $\mathbf{A}_t$  to the optimal value of the objective function along the planning horizon, is iterated upon to find the optimal policies  $x_{ijt}^*(\mathbf{A}_t)$ , i.e, the sequence of optimal treatments, and the optimal states  $\mathbf{A}_t^*(\mathbf{A}_0)$  resulting from the optimal policies and the initial conditions. However, it is impractical in our case. Our problem suffers a *dimensionality curse* (Bellman, 1957). There are  $3^{n^2}$  values for the state variables<sup>11</sup> in each period and the specific nature of our objective function  $H$  (e.g. no global convexity) and the discrete nature of the state space make interpolation of a value function impossible<sup>12</sup>.

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<sup>10</sup>"An optimal policy has the property that whatever the initial state and initial decision are, the remaining decisions must constitute an optimal policy with regard to the state resulting from the first decision". (See Bellman (1957), Chap. III.3., p.83)"

<sup>11</sup>Given that the landscape  $\mathbf{A}$  is of size  $n \times n$ , and that each element of  $a_{ij}$  can take  $c = 3$  values, there are  $3^{n^2}$  landscape configurations possible

<sup>12</sup>As a matter of fact, with a large number of state variables e.g. a high-dimensional state space, methods such as adaptive sparse grids can be used to with smooth, continuous objective functions (Brumm and Scheidegger, 2017) to circumvent the dimensionality curse. The fact that the input space is an  $n^2$ -dimensional binary Cartesian product and that  $H$  is not globally convex hinder the use of such tools.

### 3 Solution method and computational experiments

Three key features of our problem hint that a dynamic (e.g. that optimizes the objective function over the whole planning horizon) and a repeated myopic solution (e.g. which optimizes the objective function in each period) should be similar. The dynamics occur before the decision is made, therefore the decision maker has full knowledge about the state of the system. The dynamics are simplified and have relatively little depth, as we limit ourselves to 3 age classes. Finally, our intertemporal objective function is additively separable.

Our solution methods resort to two key ingredients : optimization heuristics, and comparison between the dynamic and repeated myopic problem.

First, we circumvent the non-convexity of the global connectivity metric and the high dimension of the state space by using a genetic algorithm ([Holland, 1992](#)) (implemented in R with package GA ([Scrucca, 2017](#))) with population size of 200 and 250 iterations. Genetic algorithms are especially suited for high dimensional, combinatorial search spaces<sup>13</sup> and fare better than a brute force approach, or other heuristics (Particle Swarm Optimization or Simulated Annealing).

Then, we compare the performance of a 5-period objective function to a 5 period repetition of a static objective function. We trade the completeness of dynamic programming for a more manageable approach, where we compare these approaches for 884 randomly drawn landscapes of size  $n = 4$ . We sample the landscapes according to the distribution of possible landscapes (see figure 2.C). As landscapes with large numbers of *juvenile* and *adolescent* cells are overrepresented, we impose that underrepresented possible landscapes are included at least 2 times in our sample, to disentangle composition (e.g. number of cells of each successional stage) from configuration (location of cells) effects.

We focus  $T = 5$  planning horizon for several reasons. First, as the dynamic of our ecological processes comprises 3 stages, using a 5-period horizon allows for each cell to grow from its original stage to *mature*, be treated, and revert to its original stage, e.g. allows for a full successional cycle to be performed. Second, a 5-period horizon corresponds to a long policy horizon, ranging from 25 years to 200 years ([McColl-Gausden and Penman, 2019](#); [Thomas, 1979](#)). Third, for our approach to be useful for policy making given that we abstract from stochastic modifications to the environment (e.g. occurrence of wildfire, spread of invasive species increasing flammability at a given age etc), policies need to be forward looking with enough temporal depth to be relevant and be reevaluated with potentially new initial conditions resulting from environmental perturbations.

Next, with repeated static optimization we increase the size of our sample and temporal depth, to encompass all the possible landscape configurations for land-

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<sup>13</sup>Here, the control variable is a  $Tn^2 = 5n^2$  binary variable

scape size  $n = 4$ , over the whole range of possible values for the biodiversity habitat constraint, over  $T = 10$  years. Of all the  $3^{n^2}$  initial landscapes combinations possible, we only keep landscapes that are unique up to a permutation<sup>14</sup>. This results in a sharp reduction of landscapes to consider from 43,046,721 initial to 5,398,082 unique initial landscapes for  $n = 4$ . We focus on exact optimal solutions for all the initial conditions of these small-scale landscapes and implement our own solution algorithm in Python 3.9.13 and R 4.3.3<sup>15</sup>. We find generally applicable principles for treatment allocation.

Third, we increase the landscape size to  $n = 100$ , for a sample of 20 large scale (10,000 cells) landscapes with varying compositions and autocorrelation using two-dimensional fractional Brownian motions (table 2.A summarizes their characteristics and figure 2.B illustrates 6 of them). We use neutral landscape models (Caswell, 1976; Gardner and Urban, 2007) and implement them in R (Sciaini et al., 2018). Neutral landscape models were designed in theoretical landscape ecology to develop spatial ecology indicators and “evaluate the effects of landscape structure on ecological processes” (With and King, 1997). Even though they are designed as null models to compare with real landscapes, after ecological processes have shaped them, they provide a useful basis for scaling our analysis. We solve the repeated myopic optimization problem on these 20 landscapes over  $T = 10$  periods based on our generally applicable principles, and compare them with other policy scenarios. We compare our principles with (i) a repeated random policy, targeting cells that are either *adolescent* or *mature*, (ii) a gridded treatment policy (as depicted in figure 2.F) with evenly spaced segments of treatment, (iii) a policy that always targets the most central nodes in terms of betweenness centrality, and (iv) a policy which targets the largest degree<sup>16</sup> nodes, in terms of global risk and habitat connectivity measures.

## 4 Landscape and treatment indicators

### 4.1 Landscape level indicators

To characterize the managed landscapes, we mobilize several indicators from landscape ecology and graph theory (see appendix C).

First, we account for the high risk and habitat surfaces in the landscape by measuring the number of vertices in each graph. Second, to assess landscape connectivity and fragmentation as well as landscape diversity<sup>17</sup>, we use our global

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<sup>14</sup>That is to say, landscape  $\mathbf{A}_0$  is included in the set of initial conditions  $\mathcal{I}$  if and only if for any element  $\mathbf{A}'_0$  in  $\mathcal{I}$ ,  $\mathbf{A}_0$  is not a permutation (eg can be obtained through rotations or symmetries) of  $\mathbf{A}'_0$

<sup>15</sup>Data and code are [publicly available](#)

<sup>16</sup>In a graph  $\mathcal{G} = (V, E)$ , the degree of a node  $v$  is the number of edges connected to the node

<sup>17</sup>In the context of fire prone ecosystems, the notion of “fire mosaics” (Bradstock et al., 2005)

connectivity metric  $H$  (eq. 2.4), as well as the *number of components*<sup>18</sup>. To specifically assess landscape diversity, we use the Simpson index (Simpson, 1949) on successional stages stages (eq. A.4)<sup>19</sup>. However, the Simpson index does not account for the diversity of spatial patterns: a checkered landscape with two seral stages would be as diverse as a landscape with two large patches for each seral stage, according to the Simpson index. Therefore, we use the landscape shape index (LSI - eq. A.5), a normalized ratio between the perimeter of biodiversity habitat and its area (Patton, 1975; McGarigal and Marks, 1995). To disentangle the correlated effects of perimeter and area that affect the landscape shape index, we use a successional stage heterogeneity index, that averages the probability that, for each cell, neighbors in the 4 cardinal directions share the same successional stage (eq. C). The index ranges between 0, when the successional stage is the same across the whole landscape, to 1, in a checkered landscape. The index assesses whether the landscape is a mosaic (Bradstock et al., 2005), and if it displays structural diversity, conducive to diverse communities and functional diversity.

## 4.2 Treatment level indicators

To analyze the treatment allocation mechanism, we use the *number of treatments* as well as their *geographic location*. Additionally, we use graph theory measures to assess the location of treatments in relation with the graph structure. To do so, we use different measures of *centrality*, e.g. measures that answer how important a vertex is for the graph structure, and overall, its connectivity. Measures of centrality produce a ranking of vertices, but are not necessarily comparable. Additionally, depending on the measure chosen, different vertices can be the most central. To overcome these limitations, we use 4 measures of vertex centrality.

First, we use *degree centrality*, which measures the degree of vertices. This measure is computationally simple and captures direct centrality effects e.g. how a single vertex interacts with its neighbors, without considering 2nd degree neighbors, or further relationships. Second, we use *betweenness centrality* (see appendix D for a formal definition), measuring the extent to which a vertex is on the shortest path between other vertices. This measure is more computationally intensive and useful to understand through which vertex flows may go through, e.g.

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conveys the idea that fire causes variations in successional stages through space thus providing different types of habitat for biodiversity and improving biodiversity

<sup>18</sup>A component  $C_t$  of graph  $\mathcal{G}_t$  is a maximally connected subgraph of  $\mathcal{G}_t$  that is not part of any larger connected subgraph. A component is *connected* (for all two vertices  $(u, v) \in V_C$ , there exists a path in  $C_t$  that connects them) and  $C_t$  being a subgraph of  $\mathcal{G}_t$ , it is *maximal* if there is no other connected subgraph  $C'$  of  $\mathcal{G}_t$  such that  $C_t$  is a proper subgraph of  $C'_t$ . Figure 2.2 illustrates this concepts in both the habitat and high risk graphs resp.  $B_t$  and  $F_t$

<sup>19</sup>Similar results can be found with the Shannon index (Shannon, 1948). To avoid issues related to degenerate values and logarithms, we focus on the Simpson index.

wildlife dispersal or wildfire spread. Third, we use *eigencentrality*, which measures the influence of nodes through their connections : a vertex is central if it is largely connected to nodes themselves well-connected. While computationally intensive, it furthers the results from degree centrality. Finally, we use *subgraph centrality* (Estrada and Rodríguez-Velázquez, 2005), which measures the participation of vertices to subgraphs of the graph, and captures the role of a node in local structures, especially suited for networks with well identified, low connected subgraphs. We implement these measures in R using the package `igraph` (Csárdi and Nepusz, 2006)

## 3 Results

### 1 Dynamic v. myopic repeated optimizations

As expected, the results of the dynamic and static optimization procedures over 5 periods yield very similar aggregate results in terms of intertemporal global risk connectivity (hereafter *risk*), for different budget (measured in treatment units) and global habitat connectivity constraints (hereafter *habitat constraints*, measured as proportion of the maximal global habitat connectivity attainable), as shown by figure 2.3.

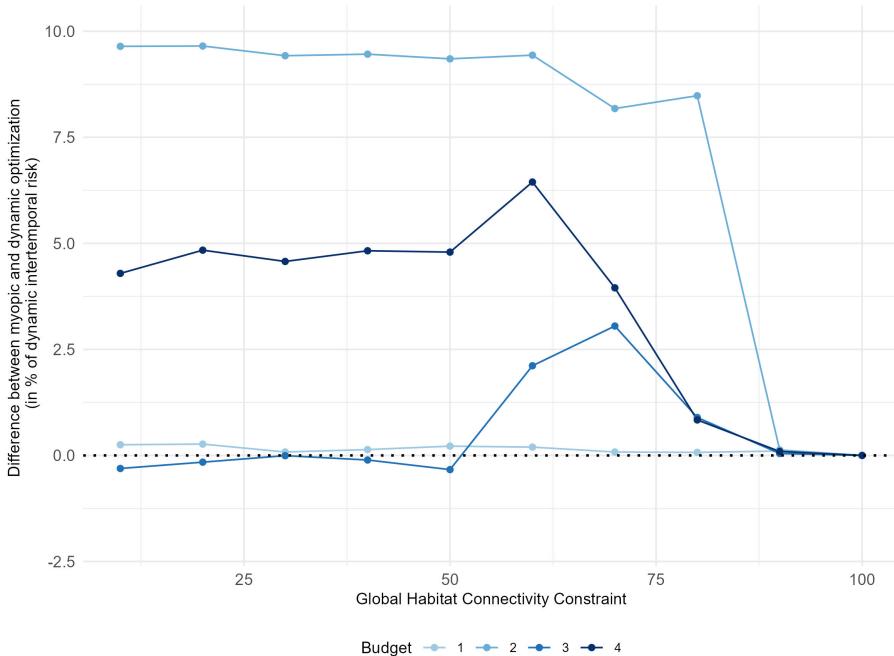


Figure 2.3: Comparison of aggregate intertemporal global risk connectivity for dynamic and repeated myopic procedures

Table 2.B shows the result of a regression analysis of the difference in global risk connectivity between the dynamic optimization and the repeated myopic

procedure (e.g. if the difference is positive, repeated optimization results in a lower intertemporal global risk connectivity), based on initial landscape characteristics, without interaction terms. First, the average risk difference is positive across all habitat constraint levels (given the magnitude of the intercept and constraint coefficients). With larger budgets, the relative performance of repeated myopic optimization increases, while it merely decreases with increases in the habitat connectivity constraint level: although statistically significant, the magnitude is negligible. Finally, the Successional Stage Heterogeneity Index is statistically significant but does not lead to significant effects due to its magnitude. Other models, including interaction terms are presented in appendix F. They all point towards the absence of clear mechanism determining the performance differentials between myopic and dynamic optimization procedures.

## 2 Wildfire risk reduction and habitat connectivity : a production possibility frontier approach

Figure 2.4 shows the global risk connectivity measure, with varying levels of global habitat connectivity and budget constraint, e.g. a production possibility frontier between risk and habitat connectivity, for the 10 years planning horizon<sup>20</sup>

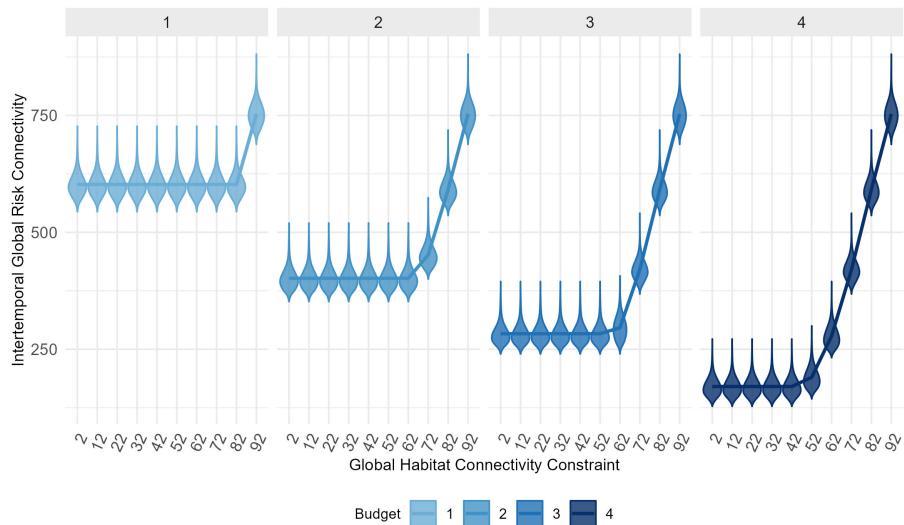


Figure 2.4: Production possibility frontier across global habitat connectivity and budget constraints

For each value of the global habitat connectivity constraint is plotted the distribution of the values in each violin plot. The line refers to the group specific average level of global risk connectivity

Using repeated myopic spatial optimization, reducing global risk connectivity while maintaining global habitat connectivity comes as a trade-off, albeit moderate: indeed, increasing habitat requirements increases the remaining risk, but

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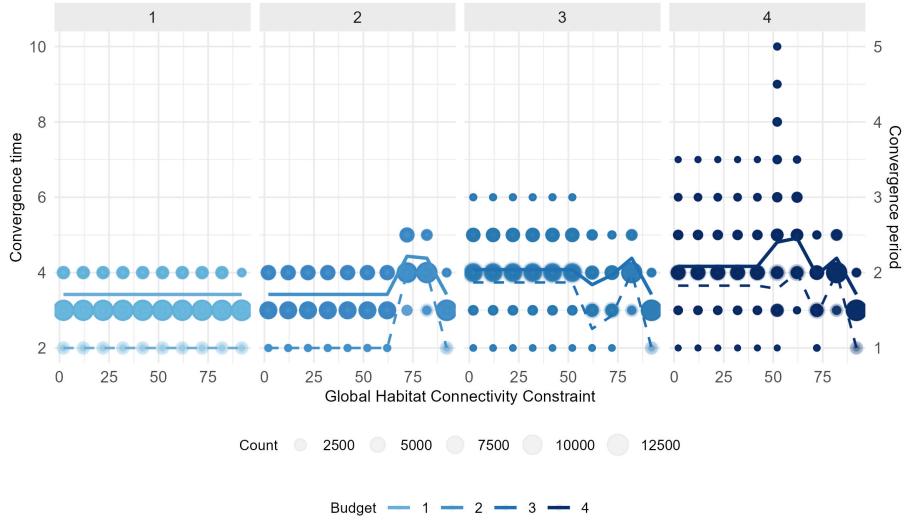
<sup>20</sup>Figure 2.D displays production possibility frontiers for repeated myopic and dynamci procedures and shows the same properties

there are combinations that can satisfy large habitat connectivity and risk reductions.

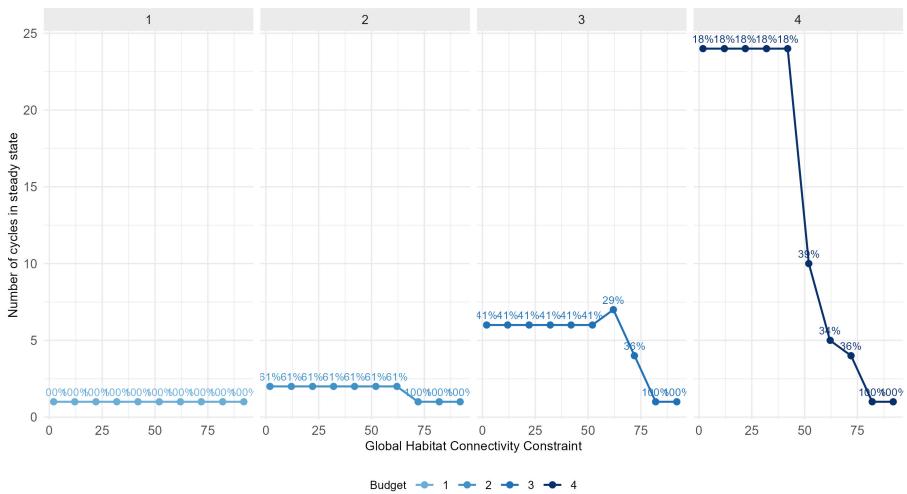
Budget is a key factor in risk reduction, as it relaxes the trade-off between the two objectives: increasing the budget reduces the wildfire risk while maintaining a range of biodiversity constraints. When habitat constraints are large, however, the marginal effect of budget is limited, production possibility frontiers tend to be identical and a larger remaining risk needs to be accepted. Indeed, when the  $Budget = 2$ , average risk is maintained at 401 for habitat constraint levels ranging from 2 to 62, while when  $Budget = 4$ , risk is down to 170 (−58%) for habitat constraint levels ranging from 2 to 42. However, when the habitat constraint is at 72, average risk for  $Budget = 2$  is at 451, while it is at 420 for  $Budget = 4$  (7% difference). Hence, similar risk profiles can be attained at a lower budget for high habitat constraints. Conversely, as the costs of treatment increase, for a stable budget, the remaining risk increases sharply, and factoring in habitat requirements in the decision-making is not necessary for targets below 82. For example, if costs were to double at  $Budget = 2$ , the average risk between 2 and 62 would increase by 50% (e.g. at  $Budget = 2$ , average risk is 401, while it is 602 for  $Budget = 1$ ), and the habitat constraint only becomes stringent at 82.

### 3 Convergence towards steady states

Our simulations for  $T = 10$  and scanning all the possible configurations for landscapes of size  $n = 4$  show that 100% of the initial landscapes converge in finite time towards a steady state solution, that minimizes wildfire risk while satisfying budgetary and habitat connectivity requirements (figure 2.5a). Steady states are landscape cycles with finite periods. Landscapes converge to steady state distributions given the bounded nature of the successional dynamics. Analyzing the steady-state cycles (and the unique landscapes that form them) drastically reduces the set of landscapes to analyze: they represent 0.001% of the initial landscapes. Results show that landscapes converge to cycles with equivalent configurations when the cycle period = 1, or have a transitory phase during 1 period, before reverting to an equivalent configuration.



(a) Convergence times and period across global habitat connectivity and budget constraints  
Average convergence time is displayed with full lines and measured on the left  $y$ -axis, while average convergence period is displayed with dashed lines and measured on the left  $y$ -axis



(b) Number of cycles in steady state as the global habitat connectivity constraint evolves and across budget constraints

Above each data point is the frequency of the most represented cycle in the data.

Figure 2.5: Steady state cycles: convergence and distribution

Figure 2.5b shows that conditional on data availability on every patch, the more the decision maker wants to conserve biodiversity, the fewer steady-state landscapes she has to consider. An increase in the habitat requirement reduces the room for maneuver. Indeed, budget acts as a complexifying factor: the larger the budget (relative to costs), the larger the set of steady-states to consider. Aiming for relatively large habitat connectivity reduces the set of viable strategies to be considered and can more efficiently guide policy.

## 4 Properties of steady state landscapes: surface, fragmentation, and diversity

Figure 2.6 displays, for each global habitat connectivity and budget constraint levels, the most frequent steady-state cycle. Figure 2.7 shows the indicators relative to the surface and components of the high-risk graph and figure 2.8 shows the indicators related to diversity, both for landscapes of size  $n = 3$  and 4, averaged over all the steady-state landscape cycles.

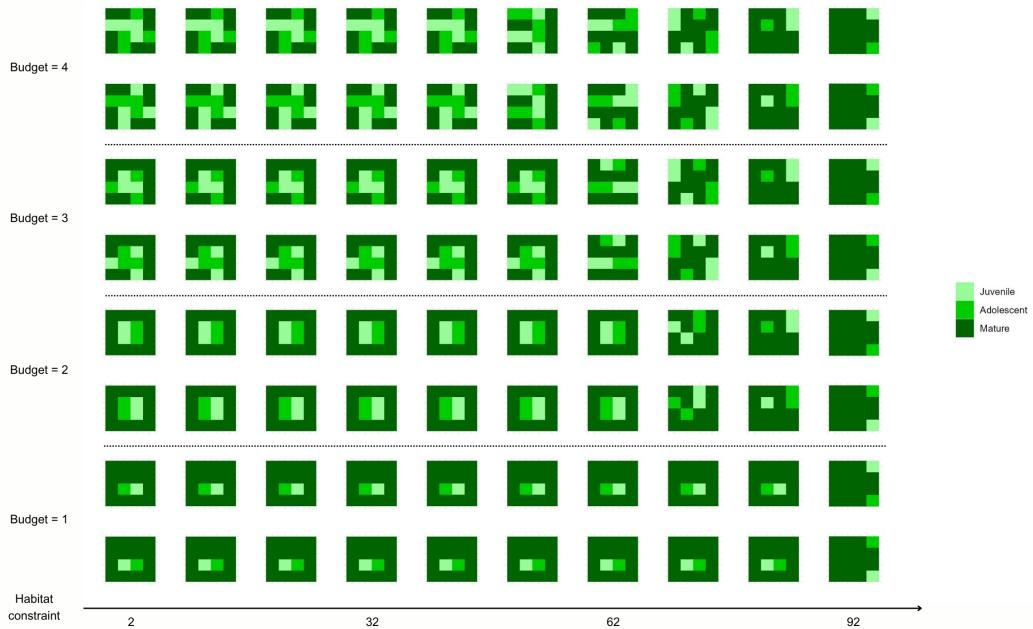
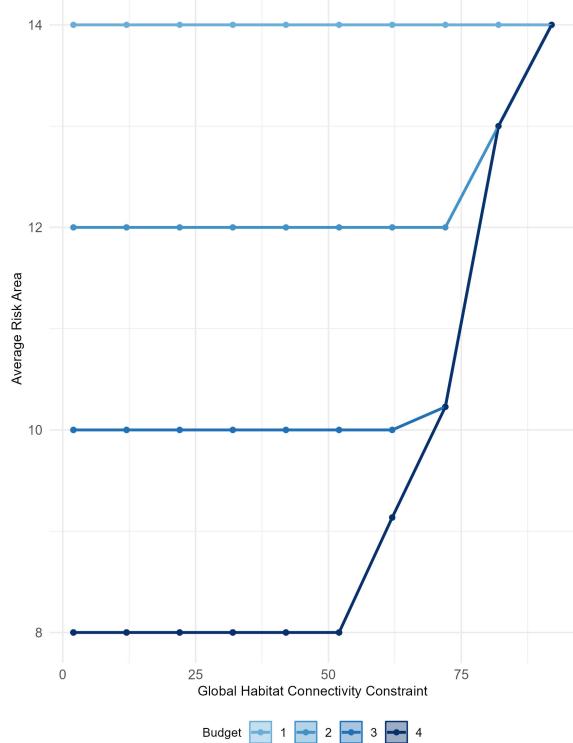


Figure 2.6: Most represented cycles for each global habitat and budget constraint levels

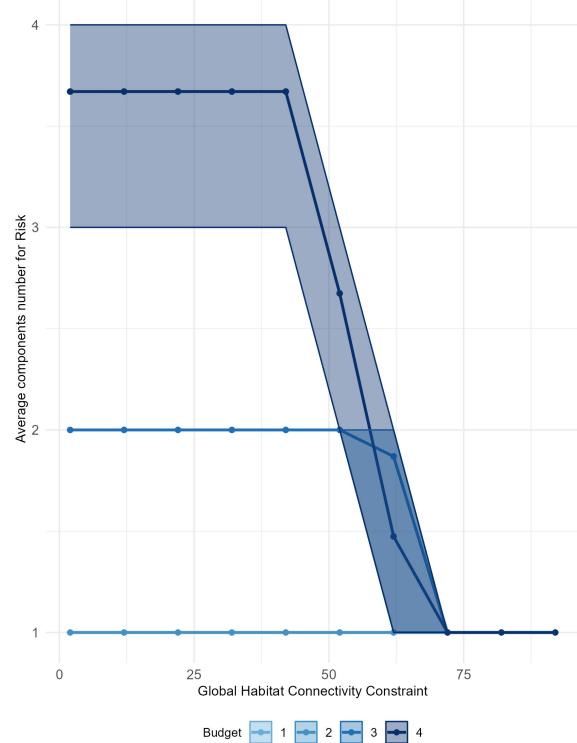
Previous results show that budget further reduces risk, conditional on habitat connectivity constraint being low. Focusing on constraint levels below 50, risk reduction is primarily driven by reduced area (figure 2.7a), and increased fragmentation of the landscape, in the form of increased components number and reduced sized of the components mean size (figures 2.7b and 2.7c). As more connected habitat needs to be protected, the average size of components increases for all  $Budget > 1$ . For large budgets (e.g.  $Budget \in \{3, 4\}$ ), the average component number starts to fall first (for example, at habitat connectivity constraint level 40 for  $Budget = 4$ ), and then the average risk area increases (for example, at habitat connectivity constraint level 52 for  $Budget = 4$ ). The average component size increases as the number of components decreases for habitat connectivity constraints above 42 : small components either disappear or increase in size, risky cells are reallocated to connect separated components before the high-risk surface increases. This is exemplified by the landscape cycles displayed in figure 2.6 (especialy for panels of  $Budget \in \{3, 4\}$ ).

Landscape diversity unambiguously increases with the budget at low habitat connectivity constraint levels (figures 2.8a and 2.8b). As more units are treated, the evenness of successional stages increases in the landscapes, which drives increases in the Simpson Index (fig. 2.8a). At low habitat connectivity constraints, global risk connectivity is diminished through fragmentation of the risky patches. The larger the budget, the more treatment, and the more fragmentation, which increases the structural diversity of the landscapes as cells are less likely to be at the same successional stage in all directions, driving the evolution of the Successional Stage Heterogeneity Index (fig. 2.8b). At low habitat connectivity constraint levels and large budgets, even though the relative area of habitat decreases, the shape of habitat is more irregular (fig. 2.8c). In this context, *adolescent* cells act as stepping stones and corridors between *mature* habitat patches.

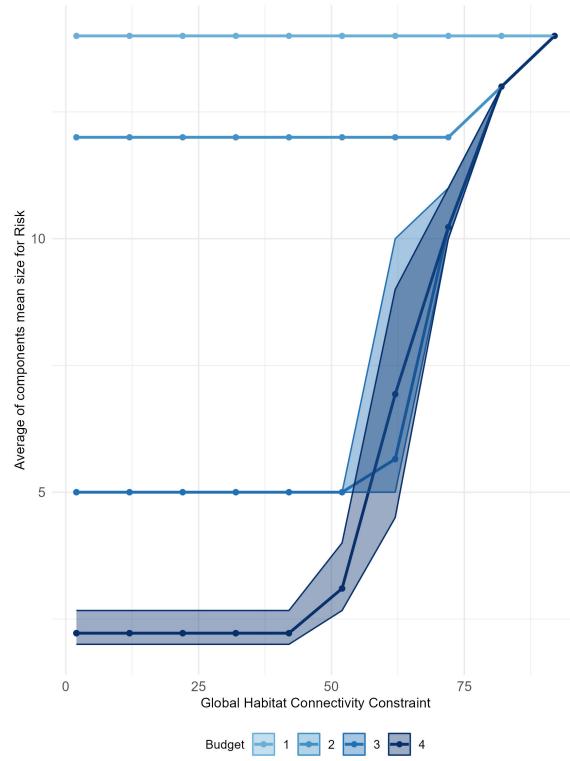
When habitat connectivity constraints increase, diversity collapses both quantitatively and qualitatively (fig. 2.8). The Simpson index collapses as land successional stages gradually homogenize (fig. 2.8a) across all budgets. Moreover, landscapes form less of a mosaic, and are more clumpy, as displayed by the LSI and Successional Stage Heterogeneity Index (figs. 2.8c and 2.8b). Overall, for large habitat targets, landscapes tend to homogenize and to be better connected, although less quantitatively and qualitatively diverse.



(a) Average area



(b) Average component number



(c) Average components size

Figure 2.7: Indicators relative to surface and components across habitat and budget constraints

The indicators are averaged across the cycles represented for each habitat and budget constraint levels.

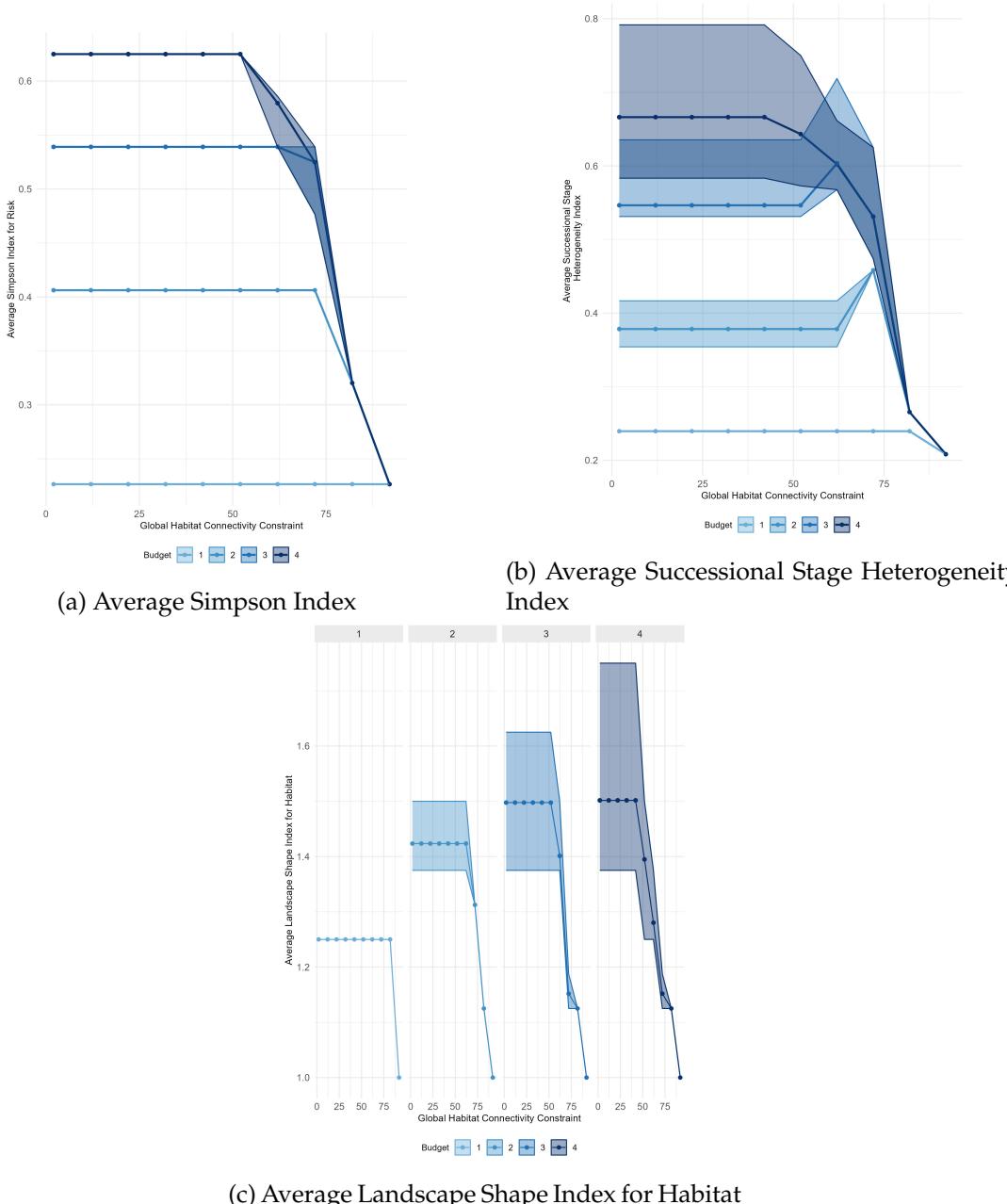


Figure 2.8: Indicators relative to landscape diversity across habitat and budget constraints

The indicators are averaged across the cycles represented for each habitat and budget constraint levels.

## 5 Spatial allocation of optimal management at the steady-state landscape cycle

Treatments are concentrated on *adolescent* cells across all budget and habitat connectivity constraints (figure 2.9, except at 62, for some steady-state cycles for  $Budget \in \{3, 4\}$ ). This is coherent with the real life practice of fuel management operations, primarily targeting *adolescent* land patches. At level 62, the number of treatment varies between phases of the steady-state cycle for  $Budget = 4$ , reflecting the increase in habitat connectivity constraint.

As shown in figure 2.10 for low habitat connectivity constraints, the budget constraint is saturated, and all of the budget is used. Coherent with the evolution of risk area highlighted in section 4, the number of treatments decreases after the steady state landscape start experiencing an increase in mean component size, and gradually reduce as the habitat connectivity constraint increases (e.g. starting at 62 for  $Budget = 2$ , or 52 for  $Budget = 4$ ): for large habitat connectivity constraints, the budget constraint is no longer satiated.

Figures 2.11a, 2.Ea, 2.Eb and 2.Ec show that the different centrality measures (e.g. betweenness, subgraph, degree and eigencentrality, respectively), are very correlated, and display identical overall patterns, in terms of relative values of metrics compared to the maximum possible, and in terms of rankings. We therefore focus on betweenness centrality to characterize our results.

Figure 2.11a shows the average betweenness centrality (and the corresponding ranking) of treated cells in risk graphs  $\mathcal{F}_t$ . For low levels of biodiversity constraint, cells with the largest betweenness centrality are treated first, as testified by the panel of  $Budget = 1$  in figure 2.11a, and illustrated by the average share of treatments per cell in figure 2.11b. Across budgets, the first treatment unit targets the most central cells when available for treatment. In the context of critical node detection, when the ecological requirements are low, the high-risk graph  $\mathcal{F}_t$  is primarily considered, and nodes with the most cost-efficient risk reduction, i.e., with the largest betweenness centrality are targeted. Once the most connected cells are treated and the budget constraint relaxes, lower-centrality cells get treated, in a sequential fashion. : for  $Budget = 4$  and constraint below 42, the first treatments across cycles are the 1<sup>st</sup> and 2<sup>nd</sup> most central locations, but the 4<sup>th</sup> treatments target the least central cells with non zero centrality. This is epitomized by the top row of figure 2.11b.

When the habitat connectivity constraint increases, several effects come at play. Not only does the number of treatments decrease, but the spatial allocation also changes. When  $Budget = 3$ , figure 2.10 shows that treatment number remains constant between habitat connectivity constraints 52 and 62, but the spatial distribution of treatments drastically changes (fig 2.11b), as treated cells are

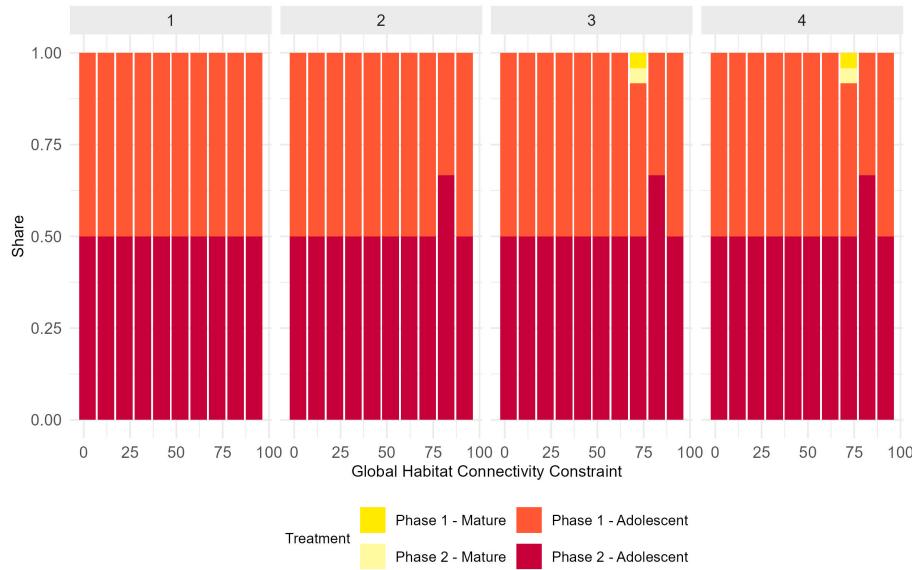


Figure 2.9: Distribution of the successional stages of treated cells in steady state cycles across budget and habitat connectivity constraints

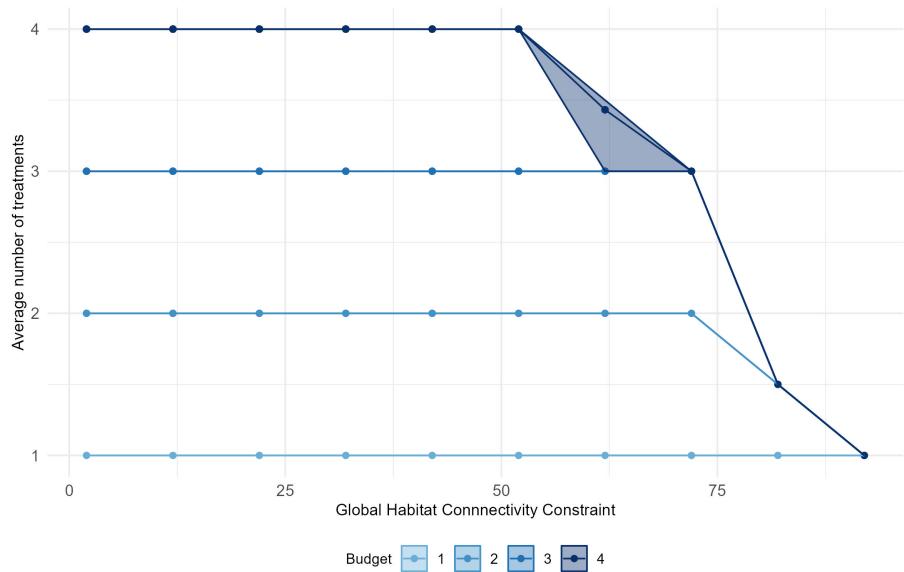
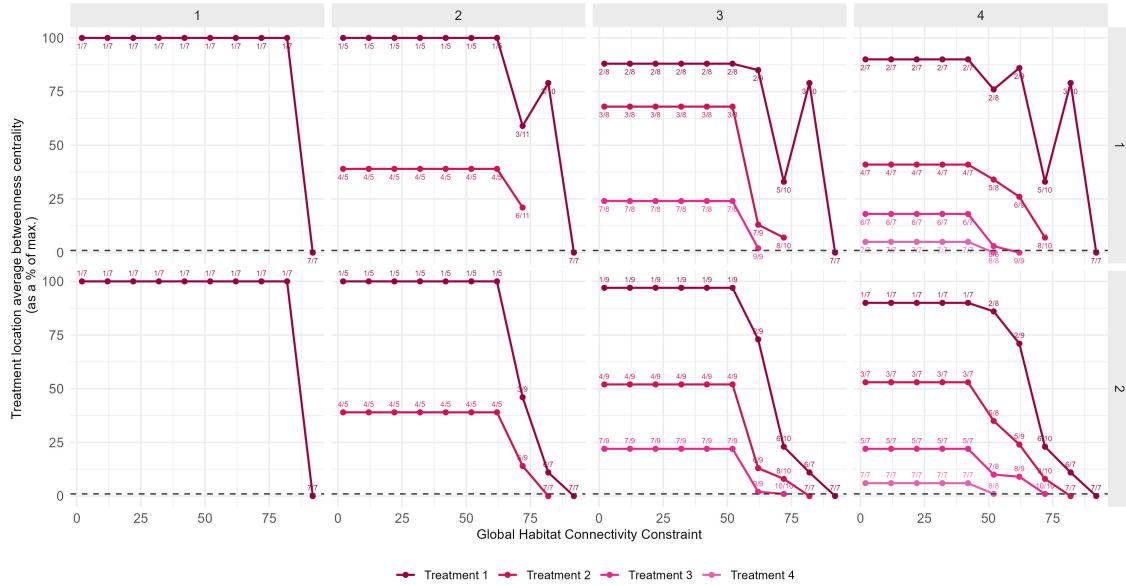
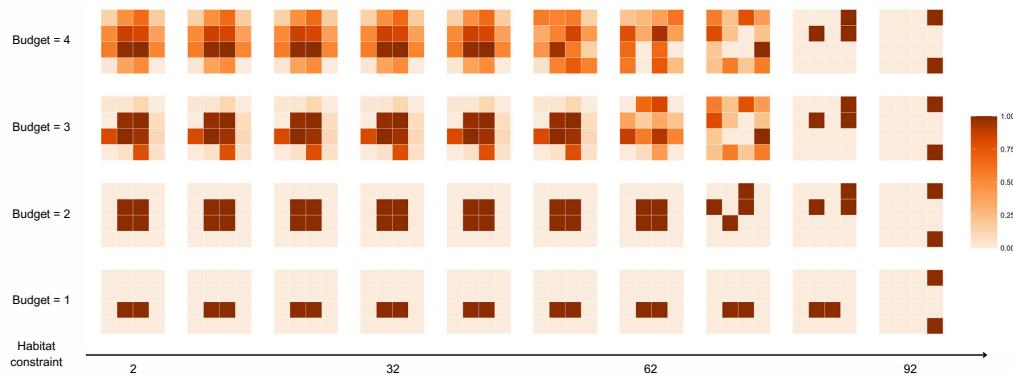


Figure 2.10: Average number of treatments in steady state cycles across budget and habitat constraints.



(a) Average treatment location betweenness centrality across budget and habitat connectivity constraints, and steady-state cycle phases

On the horizontal grid are displayed budget levels, while cycle phases are displayed on the vertical grid. For each steady-state cycle, treatment location is characterized by a betweenness centrality score, as a proportion of the maximal betweenness. Averages across steady-state cycles are displayed. Numbers in 5/7 format refer to the average betweenness centrality ranking of the treatment



(b) Distribution of treatment locations in steady-state cycles across budget and habitat connectivity constraint levels

Each cell is colored as the average of her treatment indicator  $x_{ijt}$  over all steady-state : the darker the cell, the higher the frequency of treatment

Figure 2.11: Treatment allocation : centrality

less central, and edge cells are more treated (fig 2.11a) as the relative weight of the habitat graph  $\mathcal{B}_t$  increases, treating the most cost-efficient risk-reducing nodes also degrades habitat connectivity.

Therefore, as habitat targets increase, the number of treated cells remains stable but the betweenness centrality of cells decreases : for  $Budget = 2$ , aggregate betweenness centrality starts declining at 62, for  $Budget = 4$  at 42 (figs 2.11 and 2.11b). Then, the number of treated cells decreases : for  $Budget = 2$  for example, treated cells start declining at 82, and for  $Budget = 4$  at 52 (fig 2.10). Once the number of treated cells has decreased, there is a spike in betweenness centrality of the remaining treated cells : while less area is treated, a more central location is treated (see the panel of phase 1 and  $Budget \in \{2, 3, 4\}$  at levels 82). Then, the number of treated cells continues to decrease as the habitat connectivity constraint increases, and less central cells are targeted.

Considering results in terms of pattern convergence and treatments characteristics, general treatment guidelines can be derived and applied to large scale landscape, with a budget comprised between 0 and 25% of the landscape size. As measures of connectivity can be correlated at the small scale, but differ at the large scale, we formulate 4 different strategies, where centrality is defined according to the 4 measures used :

1. For low habitat requirement (e.g. below 50% of maximal global habitat connectivity), the budget constraint must be saturated and target cells with the largest betweenness centrality. For the first 5 periods, target cells can be both *adolescent* and *mature*
2. For intermediary habitat requirements (between 50% and 75% of maximal global habitat connectivity), and low budget, the budget constraint must still be saturated, but for larger budgets, decreased by 25%. 25% of the budget can be spent on high betweenness centrality cells, but 75% of the budget must be spent on average or low betweenness centrality cells
3. For large habitat requirements (between 75% and 100%), the budget constraint must not be saturated: the percentage of treated cells must decrease to an interval between 5 and 15%, and low betweenness centrality must be targeted if any cell is to be treated.

Across all these options, to account for the transitional dynamic, target cells can be both *adolescent* and *mature* in the first 5 periods, and exclusively *adolescent* for the last 5. We use these principles to structure treatment rules for large scale landscapes, and compare them to optimal management as well as other policy rules.

## 6 Evaluating policy rules on large scale landscapes

Figure 2.12 shows the average performance of the different policy options across 20 large scale landscapes on planning horizon of 10 periods. The performance is assessed as the sum of the global risk connectivity across 10 periods and a penalty proportional to the difference between the global habitat connectivity constraint and the global habitat connectivity score across periods.

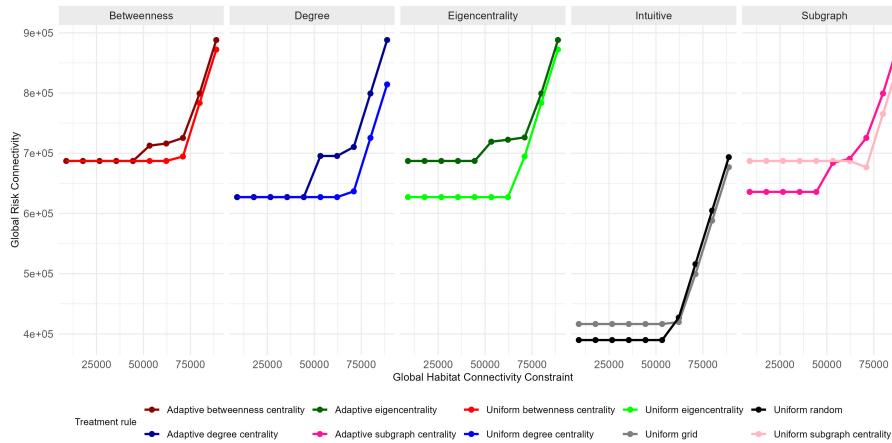


Figure 2.12: Comparison of policy intertemporal risk and penalty for large scale landscapes

The results show that the grid and random policies are always performing better than those designed based on centrality metrics, whether uniform or adaptive. Additionally, the uniform policies are always performing better than the adaptive policies. Among centrality based policies, eigencentrality and degree uniform policies are the best performing.

## 4 Discussion

### 1 Confirmation and generalization of existing results

Our analysis of the exhaustive set of initial conditions for small-scale landscapes confirms existing results in the literature. We argue that they bring robust evidence and complement the existing literature to derive general conclusions.

Our model encompasses 3 serial stages and 1 composite vegetation type and proves the convergence of every initial condition to a steady state cycle, irrespective of the initial configuration. We extend [Minas et al. \(2014\)](#) that find convergence patterns for *homogeneous* landscapes only, i.e, landscapes where the initial vegetation age is uniformly distributed. We show that in the event of environmental perturbations that do not disrupt ecosystem dynamics, an appropriate policy can recover the previous equilibrium risk and habitat.

Our production possibility frontier (PPF) between wildfire risk and habitat connectivity is consistent with PPF literature (Arthaud and Rose, 1996; Calkin et al., 2005). Our results also confirm that trading one objective for the other is not as efficient as increasing the policy budget to reconcile objectives. We show that increasing the policy budget nonetheless has diminishing returns for risk reduction, as highlighted by Wei et al. (2008); Yemshanov et al. (2021) and Pais et al. (2021b).

Our study yields clear results in terms of landscape ecology, leveraging concepts from landscape ecology, and highlighting the spatial mechanisms underlying the shape of PPF. We show that, for small scale, treatment allocation targets the most (between) central nodes first and then focuses on less central nodes (e.g cells closer to the border of the landscape) when habitat goals are low. In doing so, we do find general treatment allocation principles where previous studies on larger landscapes could not (Minas et al., 2014; Rachmawati et al., 2016), generalize smaller scale (Konoshima et al., 2008) and case study specific (Yemshanov et al., 2021; Pais et al., 2021a) results.

Compared to existing studies, our bounded depiction of vegetation dynamics allows, as well as the timing of decision making makes repeated myopic and dynamic approaches almost identical. As we abandon the refinement of dynamics, we are able to analyze the whole range of initial conditions, an endeavor that is seldom possible in dynamic spatial modeling. Using a graph theoretic framework on small-scale landscapes, we show that cell-level metrics help formalize and understand the drivers of treatment allocation and rationalize existing results.

Furthermore, we show that while prioritization approaches based on a graph theoretic framing fare very well in an unrestricted set-up, including biodiversity habitat targets augments the problem's complexity. As a matter of fact, critical node detection can be efficiently achieved (Arulselvan et al., 2009), in the presence of budget constraints. However, solving critical node detection on the risk graph  $\mathcal{F}_t$  with constraints on the habitat supergraph  $\mathcal{B}_t$  remains a challenge. We generalize case studies (Yemshanov et al., 2022) and show less central risk nodes need to be targeted to achieve risk reduction and safeguard biodiversity habitat.

## 2 Challenges in generalizing small-scale landscape rules to large-scale systems

As highlighted in subsection 6, the policy based on the results from the small scale landscapes analysis do not improve risk performances compared to random policies. Several reasons explain this phenomenon and serve as guides for future research to finalize this project.

First, on small scale landscapes e.g small scale graphs, different definitions of

graph connectivity can be highly collinear, and mechanisms to decrease different measures of connectivity tend to have the same results. However, at a large scale, this is not the case, and different connectivity measures are no longer identical. When  $n = 4$ , treating the cells with large between-centrality tends to increase the number of components of the graph. When using the proposed adaptive strategy (see fig. 2.G) and treating between-central nodes, this results in a large, donut-shaped component : the mean shortest path length between paths is increased, but not infinite, there is always a path. Hence, while betweenness centrality efficiently guides treatments to increase the number of components and reduce betweenness centrality among components on small scale landscapes, it fails at the large scale.

The performance of the gridded treatment policy (figs. 2.12 and 2.F) show that increasing the number of even-sized components is a fruitful policy option. However, the grid does not take into account initial conditions, and therefore does not *optimally* fragment the landscape. Hence, a fruitful avenue for future rules lies in having a twofold hybrid approach. First, part of the treatment budget must be dedicated to fragmenting the landscape among large scale patches. Second, the remaining part of the budget must be used to decrease within component betweenness centrality, such that global connectivity is best degraded. The method for optimal components breaking can be based on the available, budget, the distribution of the patches successional stages, as well as the distribution of the betweenness centralities of edge patches, to optimally size large components. Approaches such as Voronoi diagrams, partitioning a surface into equal sized areas from key seed points could yield interesting results. Finally, future work surrounds the use of machine learning for optimal seed detection and graph partitioning.

Second, our policy rule stems from a steady-state analysis of small scale landscapes. We have shown that small scale landscapes converge in finite time towards steady state landscapes. However, the convergence time increased with the available budget, and the convergence patterns period variance increased as well. Hence, as size and budget increase, the importance of the transition towards the steady state increases for dynamic treatment allocation and overall risk reduction. Therefore, one fruitful avenue to guide research on large landscapes can be found in analyzing the transitional dynamics of the small scale landscapes, bearing in mind the difficult scalability of specific connectivity degrading mechanisms.

### 3 Caveats and methodological perspectives

First, we resort to optimization heuristics in the dynamic and repeated cases. As the dynamic problem is significantly more complex, limiting the number of iterations of the algorithm may result in inaccuracies, which help explain the volatility of the difference in individual risk between repeated myopic and dynamic optimization procedures.

Our analysis tackles the exhaustive set of landscapes of size  $n = 4$ , allowing us to study the steady-state patterns emerging from any initial condition, replicate existing results in larger landscapes, and shed light on the mechanisms underlying the wildland dilemma.

Increasing landscape size is incompatible with this approach, as the set of possible landscapes becomes quickly unmanageable. To conserve our exhaustive approach, different proof mechanisms would be required. Nonetheless, if landscape size is of the essence for actual policy recommendation, so are other layers of information such as habitat quality, treatment costs, and values at risk heterogeneity. These other layers would reduce the computational burden, and we believe our results, targeting the most cost-efficient, risk-reducing, and habitat-conserving strategies, would still apply.

In our model, we use a simple relationship to characterize the link between the successional stage, habitat formation for a single species, and wildfire risk and severity. This choice is motivated by the existence of a lower bound for a fire return interval and drives our ability to adopt our exhaustive approach. Increasing the number of seral stages would help to complexify the relationships governing habitat formation and wildfire risk and severity: in some ecosystems, wildfire risk and severity may be higher for young vegetation than for older and may not be linear (Taylor et al., 2014). On the other hand, some species may require old-growth forests to survive, not ‘young’ forests, and old-growth forests may also be more fire-resilient (Lesmeister et al., 2021). As the number of successional stage augments, convergence towards steady-state landscape cycles would take longer, but we hypothesize it would still occur, as long as a final stage can be reached. Moreover, as long as wildfire risk and habitat quality are in conflict, a trade-off would govern treatment allocation. Multiple successional stages may be targeted for fuel treatment, depending on their location and properties, but we claim the general mechanism would still apply: in a graph weighted for different risk and habitat properties, centrality and connectivity would still guide treatment allocation.

We implicitly assume that focusing on a given species’ habitat would also provide habitat for a variety of species and be conducive to functional diversity. However, this does not imply that all species would benefit from maintaining a

given habitat type ([Saab et al., 2022](#)). Moreover, the lack of structural diversity may cause the trophic web of the targeted species to collapse. Therefore, management objectives should include structural diversity. In this case, landscapes could not satisfy extreme habitat connectivity targets and diversity targets. For intermediate goals, however, we claim that treatment allocation would still aim at fragmenting the landscape, and node centrality and connectivity would still govern allocation.

We chose to abstract from a stochastic ignition process affecting the landscape, and assumed a fully deterministic scenario. In our set-up, we assume that risk causes damages, not the realization of risk, hence we focus on a worst-case scenario. In a stochastic setting where ignition depends on the time since the last occurrence of fire, and/or the quantity of biomass in each patch, treatment location and landscape structure would be modified to account for the "free" treatments caused by fire, and the differential probabilities of wildfire occurrence. In a setting with limited successional stages, our framework is amenable to a stochastic process of wildfire. However, as we derive our conclusions from the steady-state landscape cycles, a complementary analysis of the transitional phases is required to extend our results to the stochastic case.

Focusing on the steady state, we can limit the number of landscapes to be studied. However, in doing so, we abstract away from the transitionary dynamics, which bring a lot of information on the design of optimal policies. Nonetheless, we account for transitory dynamics by relaxing conditions on the distribution of successional stages to be treated.

We use a social planner to determine the optimal allocation of treatments while safeguarding biodiversity habitat connectivity. We adopt this stance because the effects of treatments (or non-treatments) cause spatial externalities in the form of non-rival and non-excludable (e.g. public) goods (e.g. habitat connectivity) and bads (e.g. fire risk). A social planner accounts for these effects and finds the optimal location of treatments. Using a graph theoretic framework for the spatial interactions, and under the rather restrictive assumption of uniform land ownership<sup>21</sup>, our framework can be mapped to individual decisions, and how to decentralize optimal policies. Indeed, recent advances in economic theory such as [Elliott and Golub \(2019\)](#) map the position of agents in a network of public good benefits, and find how negotiating can improve the collective outcome.

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<sup>21</sup>Much like Jefferson's ideal *yeoman* democracy, this would amount to divide land in equal size patches owned by different individuals

## 4 Conclusion and policy relevance

While there is a *dilemma* for land managers between lowering wildfire risk and severity and maintaining species habitat connectivity, reconciling the two objectives is not a dead end. This is an important result for land planners as biodiversity habitat targets are gradually included in policy agendas (for example, the recent pledge by the participants to the Conference of Parties on Biodiversity in Montreal to preserve 30% of land and oceans by 2030 for biodiversity<sup>22</sup>). It shows that if policymakers can commit to a given budget over time, these biodiversity targets can be reached and a management cycle that minimizes wildfire risk can be implemented in wildlands. Moreover, as steady-state cycles are reached, the uncertainty over future land uses is resolved while achieving policy goals.

In the face of climate change, treatment costs are expected to increase ([Kupfer et al., 2020](#)). The decreasing marginal efficiency of budget to reduce risk highlights that as climate change increases the costs of treatments, risk, and damages will increase at an increasing rate, unless the budget is changed accordingly.

Our analysis shows that budget should be determined by factoring a careful, *ex-ante* analysis of treatment costs, the policy maker's risk aversion towards a measure of wildfire risk and severity, and ecological preferences. Indeed, low budget-to-cost ratios are incompatible with high risk and severity aversions and/or large ecological requirements.

As wildfires and biodiversity habitat destruction are challenges in the face of global warming, finding policy guidance tools is of the essence. Many studies focus on specific case studies or limited ranges of potential initial conditions. We develop a simplified ecological model of habitat and wildfire connectivity to guide policymakers in the form of general principles. Reducing wildfire risk and accommodating wildlife habitat is possible with carefully designed policies, where budget plays a key role. However, it is impossible to achieve drastic risk reduction without harming biodiversity habitat. General principles of treatment allocation in the landscape are derived, and the concepts of graph theory provide an operational toolbox to understand the underlying mechanisms, as well as an opportunity to connect to other branches of policy making such as economics. Landscape patches that display high wildfire risk successional stages and are well connected e.g. on the shortest path to other such patches should be treated first. When habitat targets are included, tackling lower-risk **patches** is of the essence to maintain habitat connectivity.

Our article summarizes and generalizes how policies should be implemented, both in terms of budgets and spatial allocation, to protect and enhance ecosystem health.

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<sup>22</sup>See Target 2 in the [Keunming-Montreal Global Diversity Framework, 2022](#)

## 5 Declaration

### Acknowledgments

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### Data availability

Given its size, steady-state cycle data is available upon request from the authors. Code for replication is available at [https://github.com/sim-jean/Landscape\\_connectivity\\_dilemma](https://github.com/sim-jean/Landscape_connectivity_dilemma)

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### Competing interests

The authors declare no conflict of interest.

### Contribution

LM and SJ designed the study, SJ ran the computational experiment, SJ and LM analyzed the results and wrote the manuscript.

# Appendix

## A Global connectivity index and graph theory

Minas et al. (2014) work with a collection of cells  $I$ . This landscape can be represented by a graph structure  $\mathcal{G} = (\mathcal{V}, \mathcal{E})$ . For each  $v_i \in \mathcal{V}$ , define a neighborhood<sup>23</sup> of  $v_i$  by  $\Phi_i = \{v_j \text{ such that } (v_j, v_i) \in \mathcal{E}\}$ . Finally, let  $Q_{ij} \in \{0, 1\}$  where  $Q_{ij} = 1$  if  $v_i$  and  $v_j$  are connected. Minas et al. (2014) define the following connectivity metric over a landscape:

$$z_t^* = \sum_{i \in I} \sum_{j \in \Phi_i} Q_{ij} \quad (\text{A.1})$$

For the proof, assume  $Y \in \{0, 1\}^{n^2}$  such that  $Y_i = 1$  if cell  $i$  is 'high risk' and 0 otherwise, and that we focus on the high risk graph on the landscape. The argument is identical in the case of mature habitat.

In graph theory, an adjacency matrix  $\mathcal{K}$  for an undirected graph is a binary, symmetric, square matrix of dimension  $\text{card}(V)^2$  where  $k_{ij} = 1$  if vertices  $i$  and  $j$  are connected, 0 otherwise. In our context, it is clear that  $k_{ij} = Q_{ij}$ . Equation A.1 can be reformulated as :

$$\begin{aligned} Y' \mathcal{K} Y &= \sum_j \left( Y_j \sum_i Y_i k_{ij} \right) \\ &= \sum_j \sum_i (Y_j Y_i k_{ij}) \end{aligned}$$

And notice that  $Y_j Y_i k_{ij} = Q_{ij}$ , so :

$$\begin{aligned} Y' \mathcal{K} Y &= \sum_{i \in I} \sum_{j \in \Phi_i} Q_{ij} \\ &= \sum_j \left( Y_j \left( Y_j k_{jj} + \sum_{i \neq j} Y_i k_{ij} \right) \right) \end{aligned}$$

Given the symmetric nature of  $\mathcal{K}$ ,  $\forall i \neq j, k_{ij} = k_{ji}$ . Each cell is connected to itself

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<sup>23</sup>Notice that *belonging to the neighborhood of* is a symmetric binary relationship e.g. if  $v_i \in \Phi_j \iff v_j \in \Phi_i$ , as we are working with undirected graphs

so  $k_{jj} = 1$ . Additionally, as  $Y_i \in \{0, 1\}$  then  $Y_i^2 \in \{0, 1\}$ :

$$\begin{aligned} Y' \mathcal{K} Y &= \sum_j \left( Y_j^2 + \sum_{i \neq j} Y_i Y_j k_{ij} \right) \\ &= \sum_j Y_j + \sum_j \left( \sum_{i \neq j} Y_j Y_i k_{ij} \right) \\ &= \sum_j Y_j + \sum_j d_j \end{aligned}$$

The first sum is the number of high risk cells, i.e.  $\text{card}(\mathcal{V})$ . In the second sum,  $\sum_{i \neq j} Y_j Y_i k_{ij}$  is the degree of each vertex  $j$  excluding self loops. In a graph with no self loops, by definition,  $\sum_j d_j = \text{card}(\mathcal{E})$ .

Hence, for a set of cells  $I$  reformulated in terms of graph theory :

$$\sum_{i \in I} \sum_{j \in \Phi_i} Q_{ij} = \text{card}(V) + 2\text{card}(E) \quad (\text{A.2})$$

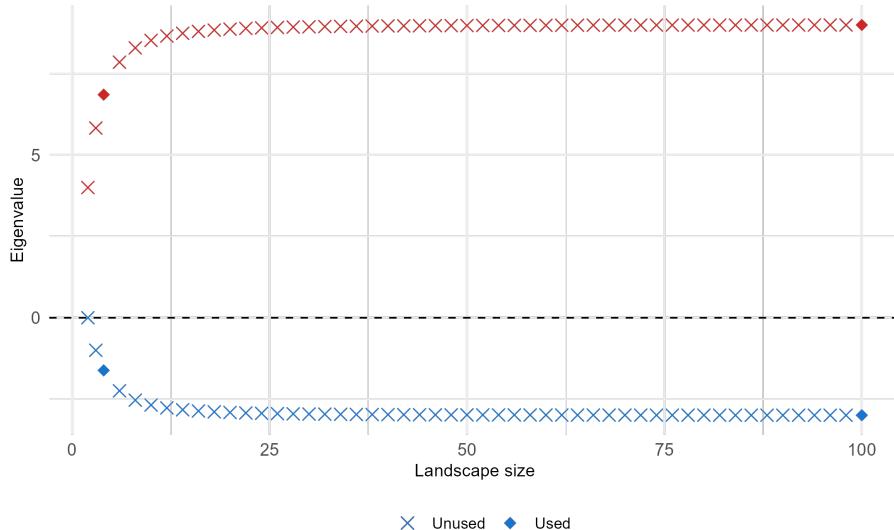


Figure 2.A: Maximum and minimum eigenvalues of  $\mathcal{K}$  depending on graph size

In red, the maximum eigenvalues, in blue, the minimal eigenvalues. Diamond-shaped points represent values actually used for the present study. Dotted line at 0

## B Large scale landscape characteristics

Age classes			Autocorrelation
<i>Juvenile</i>	<i>Adolescent</i>	<i>Mature</i>	
33%	33%	34%	0.5
10%	45%	45%	0.7
10%	10%	80%	0.9
10%	80%	10%	1.3
			1.8

Table 2.A: Summary of the large scale simulated landscapes characteristics

For each distribution profile governing the number of cells in a landscape, all of the spatial autocorrelation values are applied making  $4 \times 5$  landscapes

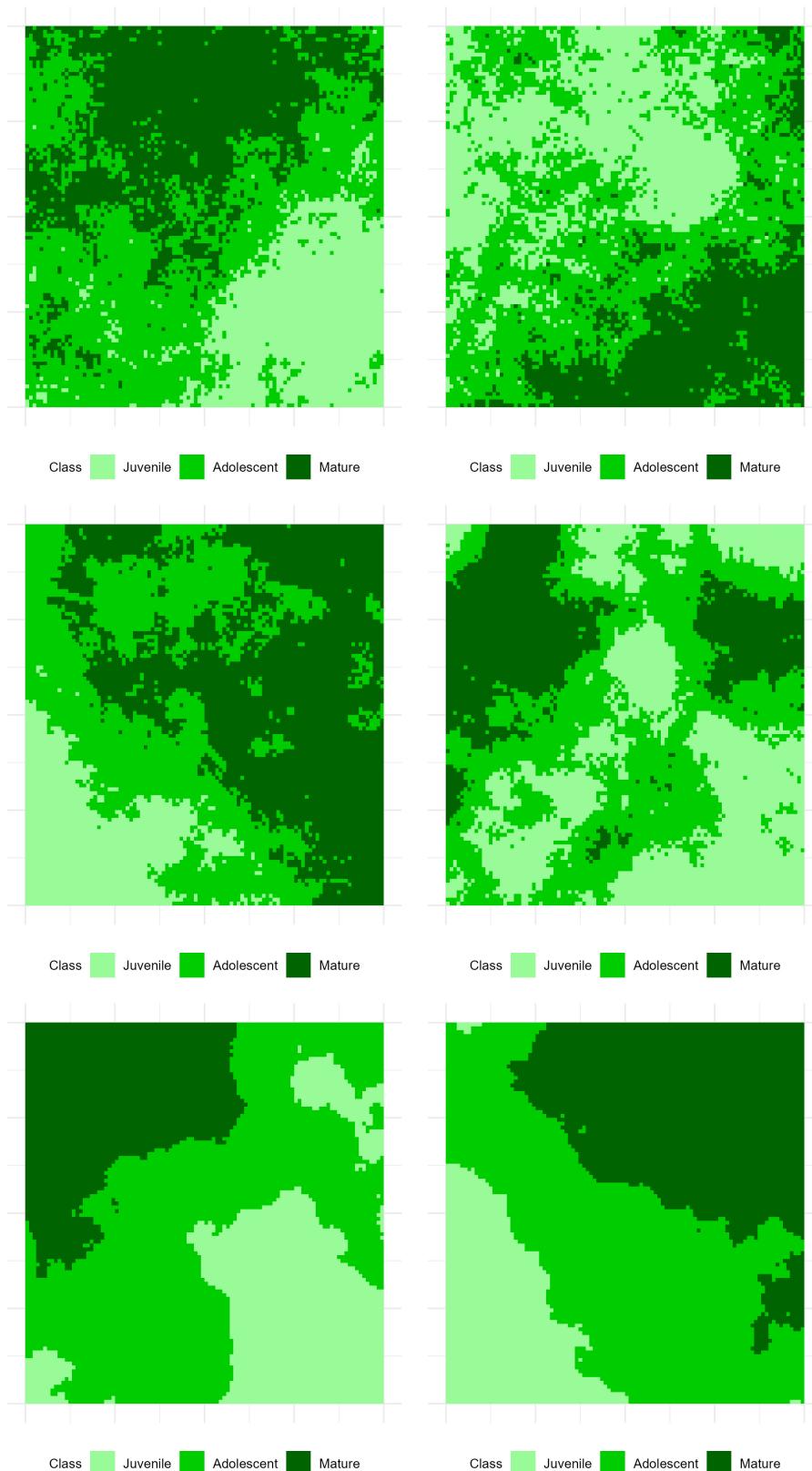


Figure 2.B: Examples of large scale landscapes

Uniform distribution (left) and skewed towards *adolescent* (right) and low, middle and large spatial autocorrelation

## C Landscape indicators

**Area** We use the number of vertices (nodes) for both graphs:

$$Area(\mathcal{G}_t) = \text{card}(V_{\mathcal{G}_t}) \text{ with } \mathcal{G}_t \in \{\mathcal{B}_t, \mathcal{F}_t\} \quad (\text{A.3})$$

**Simpson diversity index:** Let  $p_i$  be the proportion of landscape  $A_t$  in a given successional stage<sup>24</sup>, the Simpson diversity index is :

$$SIDI = 1 - \sum_{i \in \{Juv, Ado, Mat\}} p_i^2 \quad (\text{A.4})$$

**Landscape shape index:** following McGarigal and Marks (1995), the adapted LSI index from Patton (1975) in a raster landscape is:

$$LSI = \frac{0.25 \times \text{perimeter}(G)}{n} \quad (\text{A.5})$$

Where  $\text{perimeter}(G)$  is the perimeter of the cells comprised in the graph as vertices.

**Successional Stage Heterogeneity Index:** let  $d_{ij}$  be a binary variable such that  $d_{ij} = 1$  if patch  $i$  and  $j$  share the same successional stage. Define  $\mathcal{J}$  as the set of neighbors in 4 directions (north, south, east, west) of cell  $i$ <sup>25</sup>. The successional stage heterogeneity index is :

$$SSHI = 1 - \frac{1}{N} \sum_{i=1}^N \left( \frac{\sum_{j \in \mathcal{J}_i} d_{ij}}{\text{card}(\mathcal{J}_i)} \right) \quad (\text{A.6})$$

---

<sup>24</sup>Let  $Juv = \{a_{ijt} \text{ such that } a_{ijt} = 0\}$ , then  $p_{Juv} = \frac{\text{card}(Juv)}{n^2}$

<sup>25</sup>The set  $\mathcal{J}_i$  varies with cell  $i$  to account for edge effects

## D Treatment centrality indicators

**Betweenness centrality:** take a graph  $\mathcal{G}(V, E)$  and let  $\sigma_{st}$  be the total number of shortest paths from node  $s$  to  $t$  and  $\sigma_{st}(v)$  be the number of those paths that pass through  $v$ , for  $\{s, t, v\} \subset V$ , betweenness centrality is given by :

$$g(v) = \sum_{s \neq v \neq t} \frac{\sigma_{st}(v)}{\sigma_{st}} \quad (\text{A.7})$$

**Eigencentrality:** let  $\mathbf{A} \in \mathcal{M}_{n,n}$  be the adjacency matrix of graph and  $a_{i,j} = 1$  if vertices  $i$  and  $j$  are connected. Let  $\lambda \in \mathbb{R}^{n^2}$ , and a vector  $\mathbf{x} \in \mathbb{R}^{n^2}$ , such that  $\lambda \mathbf{x} = \mathbf{Ax}$  e.g  $\lambda$  is the eigenvalue of matrix  $\mathbf{A}$ . Using this eigenvalue, *centrality scores* are computed as :

$$\text{score}(x_i) = \frac{1}{\lambda} \sum_{j \in V_{\mathcal{G}_t}} a_{i,j} x_j \quad (\text{A.8})$$

**Subgraph centrality:** In a graph, a *walk* is a sequence of adjacent vertices in a graph. A *closed walk* is a walk with identical beginning and ending vertices, and can be of order  $k$  e.g. of length equal to  $k$  edges. The number of *closed walks of order  $k$*  is found using the adjacency matrix  $\mathbf{A}$  of a graph. Let  $\mu_k(i)$  be the number of closed walks of order  $k$  starting at  $i$  :

$$\mu_k(i) = (\mathbf{A}^k)_{i,i}$$

Subgraph centrality is defined as :

$$SC(i) = \sum_{k=0}^{\infty} \frac{\mu_k(i)}{k!} \quad (\text{A.9})$$

[Estrada and Rodríguez-Velázquez \(2005\)](#), who define this notion, show that it can be reformulated with the eigenvalues and eigenvectors of the adjacency matrix  $\mathbf{A}$  of a graph  $\mathcal{G}(V, E)$  of order  $n$ . Let  $v_1, \dots, v_n$  be a an orthonormal basis of  $\mathbb{R}^N$  composed of eigenvectors of  $\mathbf{A}$  associated to the eigenvalues  $\lambda_1, \dots, \lambda_N$ , and let  $v_j^i$  be the  $i$ -the component of  $v_j$ , then subgraph centrality can be expressed, for all  $v \in V$ :

$$SC(i) = \sum_{j=1}^N (v_j^i)^2 e^{\lambda_j} \quad (\text{A.10})$$

## E Additional figures

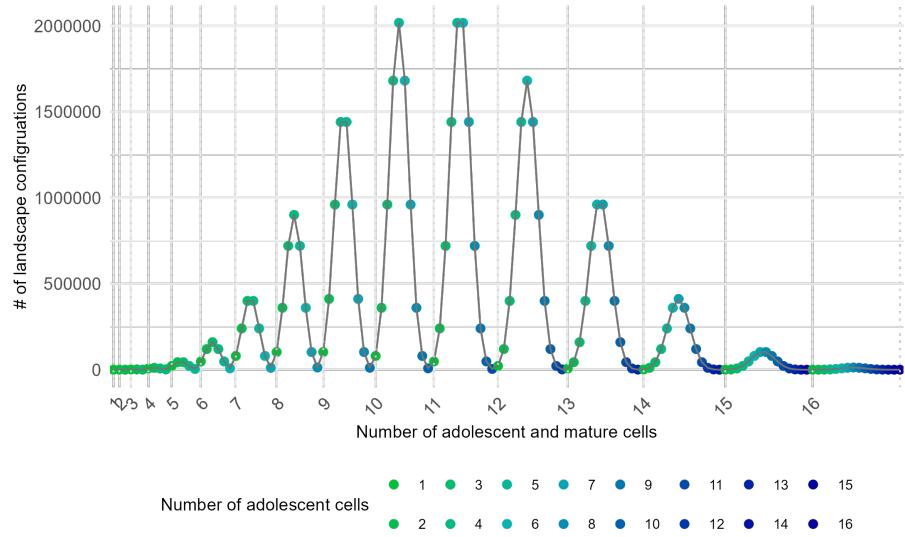


Figure 2.C: Distribution of number of landscapes depending on number of *juvenile, adolescent, and mature* cells for sizes  $\in \{3, 4\}$

Each number on the  $x$  axis represents the cumulated number of *adolescent and mature* cells among the landscape. Between each number on the  $x$ -axis is the number of *adolescent* cells among the number of cumulated *adolescent and mature* cells. For example, the highest point of the distribution, between 11 and 12, represent the number of possible combinations of landscapes with a cumulated number of *adolescent and mature* cells of 11, with 5 and 6 *adolescent cells* e.g. 6 and 5 (respectively) *mature cells*

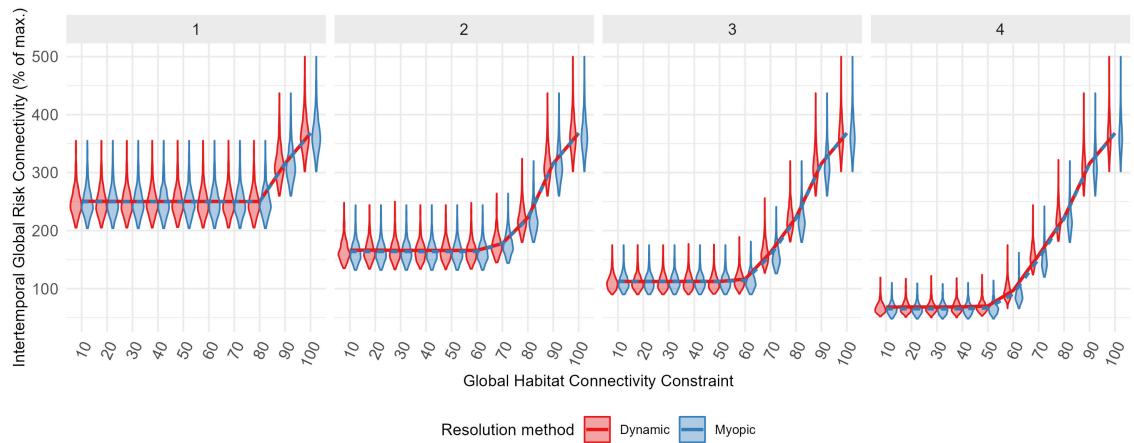
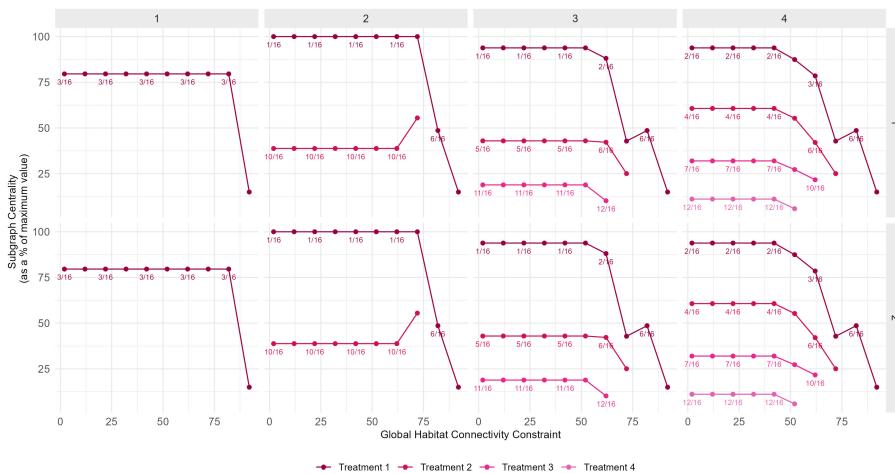
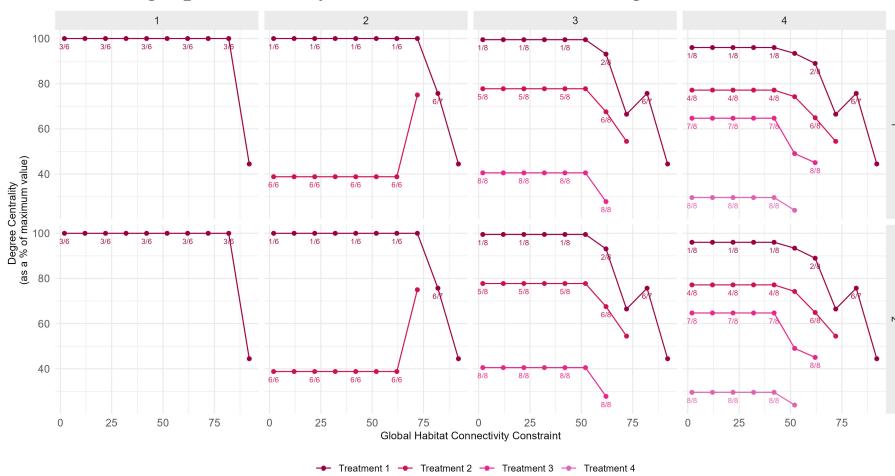


Figure 2.D: Production possibility frontiers between global risk connectivity and global habitat connectivity constraints between repeated myopic and dynamic optimization procedures for  $T = 5$

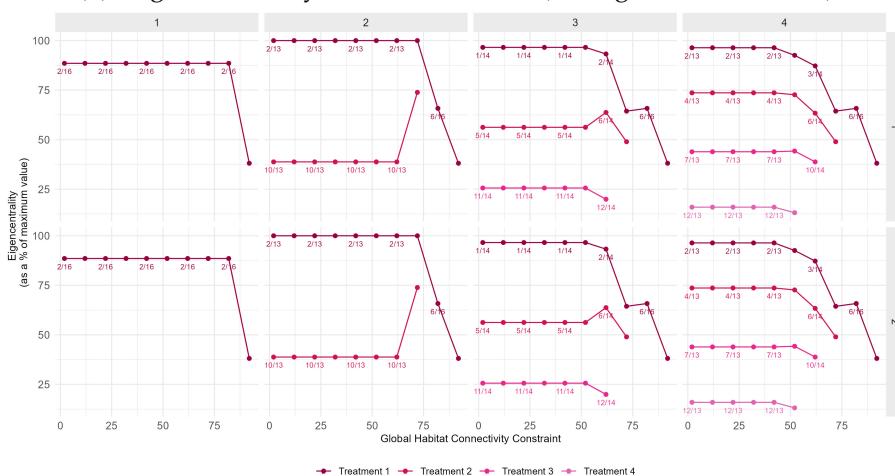
Panels represent different budget constraint levels for the sample of representative landscapes of size  $n = 4$



(a) Subgraph centrality of treated vertices (average value and rank)



(b) Degree centrality of treated vertices (average value and rank)



(c) Eigencentrality of treated vertices (average value and rank)

Figure 2.E: Average subgraph and degree centralities, and eigencentrality, across steady-state cycles for budget and global habitat connectivity constraints

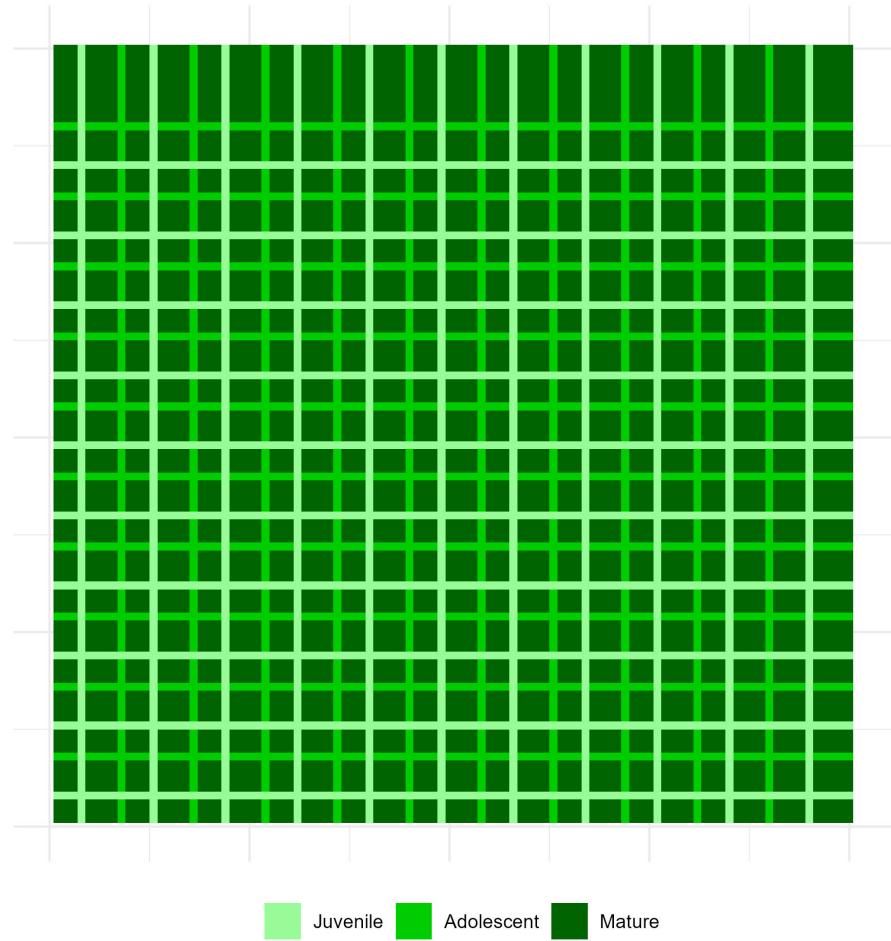


Figure 2.F: Illustration of grid treatment rule

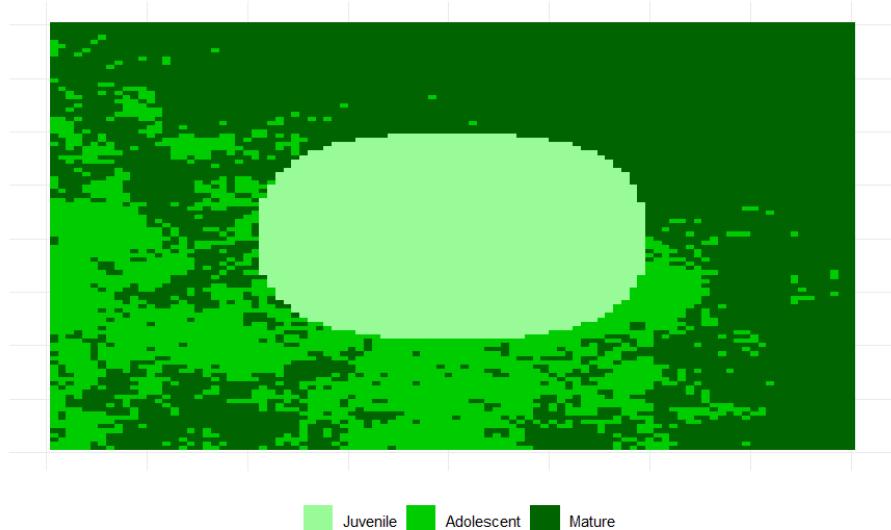


Figure 2.G: Example of location of treatment with adaptive policy on large scale landscape

## F Additional tables

The main model is :

$$\begin{aligned} DiffRisk_i = & \beta_0 + \beta_1 Budget_i + \beta_2 Constraint_i + \beta_3 Number2_i \\ & + \beta_4 LSI_i + \beta_5 Simpson_i + \beta_6 SSHI_i + \beta_7 NumberComponents_i \\ & + \beta_8 GlobalRiskInitial_i \end{aligned} \quad (\text{A.11})$$

A second model is tested :

$$\begin{aligned} DiffRisk_i = & \beta_0 + \beta_1 Budget_i + \beta_2 Constraint_i + \beta_3 LSI_i + \beta_4 Simpson_i \\ & + \beta_5 SSHI_i + \beta_6 GlobalRiskInitial_i + \beta_7 Constraint_i \times Budget_i \\ & + \beta_8 LSI_i \times SSHI_i + \beta_9 LSI_i \times Simpson_i \\ & + \beta_{10} Constraint_i \times GlobalRiskInitial_i \\ & + \beta_{10} Constraint_i \times GlobalRiskInitial_i \\ & + \beta_{11} Budget_i \times GlobalRiskInitial_i \\ & + \beta_{12} Constraint_i \times Budget_i \times GlobalRiskInitial_i \end{aligned} \quad (\text{A.12})$$

Table 2.B: Summary of model A.11: linear regression of risk differences between optimization procedures on landscape characteristics

	<i>Dependent variable:</i>
	<i>DiffRisk<sub>i</sub></i>
Constraint	−0.009*** (0.001)
Budget	0.753*** (0.030)
Number of 2s	0.034 (0.081)
LSI	−0.139 (0.230)
Simpson	−0.654 (0.618)
Successional Stage Heterogeneity Index	−0.990** (0.490)
Number of components	−0.048 (0.075)
Global Risk Connectiivty	0.002 (0.020)
Constant	1.183*** (0.270)
Observations	25,840
R <sup>2</sup>	0.028
Adjusted R <sup>2</sup>	0.027
Residual Std. Error	5.375 (df = 25831)
F Statistic	91.470*** (df = 8; 25831)

*Note:* \*p<0.1; \*\*p<0.05; \*\*\*p<0.01

Table 2.C: Summary of model A.12: linear regression of risk differences between optimization procedures on landscape characteristics

	<i>Dependent variable:</i>
	<i>DiffRisk<sub>i</sub></i>
Constraint	−0.008* (0.005)
Budget	0.661*** (0.108)
LSI	0.584 (0.643)
Succesional Stage Heterogeneity Index (SSHI)	1.087 (2.203)
Simpson	−1.612 (2.532)
Global Risk Connectivity	−0.022 (0.023)
Constraint × Budget	0.0002 (0.002)
LSI × SSHI	−1.446 (1.605)
LSI × Simpson	0.201 (2.018)
Constraint × Global Risk Connectivity	0.0002 (0.0004)
Budget × Global Risk Connectivity	0.017** (0.009)
Constraint × Budget × Global Risk Connectivity	−0.0002 (0.0001)
Constant	0.662 (0.647)
Observations	25,840
R <sup>2</sup>	0.028
Adjusted R <sup>2</sup>	0.027
Residual Std. Error	5.375 (df = 25827)
F Statistic	61.872*** (df = 12; 25827)

Note:

\*p<0.1; \*\*p<0.05; \*\*\*p<0.01

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# Chapter 3

## Fences - The economics of connectivity in spatial renewable resources

This article examines the management of spatially distributed renewable resources—specifically wildlife and infectious diseases—through the lens of economic and spatial analysis. I focus on "bads" like invasive species and diseases, which cause economic and ecological harm, and utilize population control and fencing as central mechanisms. I analyze how fencing influences resource flow and connectivity. On the one hand, in the presence of ecological and economic heterogeneities, fencing can be used to leverage spatial arbitrage opportunities. On the other hand, while promoted as a tool to incentivize the internalization of costs associated with "bads", they may undo what Nature has rightfully done. In this sense, while fencing may be welfare improving in a setting with initially poor connectivity, an uncoordinated use of fencing, although welfare improving, is not welfare maximizing. The study develops a theoretical model that integrates aspects of stock and patch connectivity management and explores both cooperative and non-cooperative management strategies. The findings indicate that optimal management often requires a nuanced understanding of the spatial dynamics and economic costs associated with different control strategies. We present a series of propositions that characterize the conditions under which fencing and resource control strategies can be optimized, including the interaction effects of exclusionary and trap effects. This article contributes to the literature by highlighting the role of spatial heterogeneity in the management of renewable resources and providing insights into the formulation of more effective environmental policies, as it analyzes how to design policies on a subset of the landscape, to maximize economic and ecological benefits.

*JEL codes :* Q20, Q24, R12

**Keywords :** spatial resource management, invasive species; fencing and control strategies; optimal management; non-cooperative equilibrium; second-best policy.

# 1 Introduction

In the Middle Ages in Europe, wildlife fencing primarily served to enclose aristocratic hunting reserves, such as deer parks or chases, where game like deer, boar, and rabbits were kept for the elite. These enclosures, often protected by wooden or stone barriers called *pales*, not only preserved game but also safeguarded nearby farmland from wildlife incursions. However, these enclosures contributed to social tensions, as peasants were prohibited from hunting within them, and wandering game often damaged crops. A notable example is the [New Forest](#) in England, established by William the Conqueror in 1079, where fencing symbolized the legal and social privileges of the nobility ([Rackham, 1987](#)).

Centuries later in the US, populations of white tailed deers have skyrocketted to an estimated 36 million, with exceptionally high densities in the South East ([Hanberry and Hanberry, 2020](#)). At high densities, deer populations threaten the regeneration of forests as they influence species composition and abundance through browsing, hence damaging people's properties ([Hanberry and Abrams, 2019](#)). Moreover, risks of zoonosis and epidemics increase with large populations. While large scale culling policies have been implemented, landowners have increasingly resorted to other methods, such as repellents, or fencing. Eight-foot or higher woven-wire fences have been used to protect agricultural land such as orchards or vineyards as well as private homes, to limit the damage done by growing deer populations ([Caslick and Decker, 1979](#)).

Eventually, during the COVID 19 pandemic between 2019 and 2023, international airports and ports were shutdown, and extensive lockdown policies were implemented worldwide. By avoiding contact between infected and non-infected people, these policies aimed at slowing the spread of the pandemic<sup>1</sup>, while managing the extent of the economic losses associated with frozen national and international economies.

These three examples display cases of management of spatially distributed renewable biological entity, species or virus, a renewable resource, either good or bad in time. Indeed, deer populations and pandemics grow through time, depending on the size of the population and location specific characteristics. Moreover, they move through land, jurisdictions and countries. These examples highlight that the management of spatially distributed renewable resources, whether goods or bads, involves at least two layers : managing the population, and how it moves through space. Indeed, culling and hunting deer population, and curing patients act as population management measures, repellents and fences keep the

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<sup>1</sup>In a given population, where successive infections are possible, lockdown policies aim at diminishing the basic reproduction number  $\mathcal{R}_0$ , which measure "expected number of infections generated by a single and (typical) infected individual during their entire infection period" see [Saldaña and Velasco-Hernández \(2022\)](#) for a primer SIR modeling applied to COVID 19

deers away (or within) and lockdowns avoid virus spread from infected to non infected people. Finally, in all cases, policies aimed at managing the movement of the resource are more efficient in one way than the other : wildlife exclusion fencing often have doors to let animals escape, and to a certain extent, people were prohibited from entering a country more than leaving one during the COVID 19 pandemic.

These examples highlight the necessity to encompass both population and connectivity management when analyzing spatially distributed renewable resources, as they raise a number of challenges. First, the decentralized management of spatially distributed renewable resources is made difficult by the spatial externality they generate. Deer are an example of species whose status depend on people's preferences and assets. When communities compete for mobile deer, they anticipate part of the herd to migrate to other communities, and tend to overharvest, as they do not have secure property right over the whole resource through time ([Kaffine and Costello, 2010](#)). When deer are bards, free riding on neighbor's culling may deters people to cull the population to efficient levels ([Costello et al., 2017](#)). In this sense, patch connectivity, in a non cooperative setting, generates inefficiencies. As a consequence, fences appear as welfare improving, as they diminish patch connectivity and therefore contribute to solving the spatial externality. If a deer herd no longer migrates, communities would tend to harvest it in a more sustainable way. If on a given property, deer have no chance of re-entering, then one may undertake efficient culling measures. However, from a welfare perspective, fencing may undo what nature has rightfully done. Considering spatial heterogeneity in marginal returns to harvesting or culling, and biological productivity, a resource may flow naturally flow to where it is best managed. In this case, although fencing can solve the spatial externality and promote efficient resource use, it would not maximize welfare. Second, spatially distributed renewable resources live on intricate institutional maps, between private and public land and sea. As a result, optimal harvesting and fencing may be difficult to decentralize. Hence, figuring the second best policy mix to best manage spatially distributed renewables is a challenge.

In this article, I focus on the management of "bads", e.g. species that cause economic damages. This includes rodents, feral pigs, deer, or predators in areas where native species prey are threatened. I develop a theoretical model *à la* [Costello et al. \(2017\)](#), to understand the interplay between stock and patch connectivity management. Species are controled, grow and disperse through space, according to immutable environmental factors and expenditures that change connectivity, e.g. fences. Fences have two effects : they keep the bad out (*exclusionary* effect), and they keep the bad in (*trap* effect). In what follows, I assume the exclusionary effect dominates the trap effect. In most cases, exclusionary fencing

keeps predators, or damaging species out, while allowing entrapped animals to leave the area<sup>2</sup>. I analyze how the changes in local fencing patterns have local and spillover effects, and can be seen as changing multilateral resistance terms in an ecological context, and show how they affect each patch, under various management regimes. This approach can be viewed as an application of the spatial trade literature to ecological networks. For example, [Donaldson and Hornbeck \(2016\)](#) shows that railroads have a global effect, as they change the "market access" of each county, accounting that local changes in "market access" have spillover effects onto other counties. More generally, to understand the general equilibrium effect of domestic policies on international trade patterns, the use of a structural gravity model is inevitable (e.g. 'the new quantitative trade model' e.g. [Arkolakis et al. \(2012\)](#)). However, the gravity equation fails at identifying the impact of country specific determinants of trade flows, e.g. multilateral resistance terms ([Anderson and van Wincoop, 2003](#)).

My contributions in this article are several. First, I characterize the value of dispersal in settings with exogenous dispersal. I outline the conditions under which connectivity changes the value of managing a spatially distributed public bad. In doing so, I outline the opportunity to consider the management of connectivity as a policy option to minimize aggregate damage, and that unless prohibitively costly, it is likely that decentralized decisions affect connectivity patterns. Second, I study the optimal policy mix between stock and dispersal rate management. When costs of control are heterogeneous, the sole owner leverages the spatial arbitrage opportunity, and when fences only have an exclusionary effect, the sole owner redirects the population stock to where it's controlled at the cheapest cost. In doing so, she reduces the population in more expensive patches further than when connectivity cannot be managed. Allowing for resource redispach, she controls more of the species. When fencing has both an exclusionary and trap effect, cost heterogeneity does not suffice to redirect the resource. If biological productivity is larger in relatively costlier patches, trapping them can increase the aggregate cost of the invasive species. Therefore, depending on the structure of dispersal and how fencing affects it, fencing occurs when biological productivities and control costs are inversely correlated.

Second, I characterize the non cooperative equilibrium in harvesting and fencing. When fencing only displays an exclusionary effect, and fencing is costless, every patch owner fences to the maximum. In doing so, they isolate their patch from the rest of the landscape, and control as if they were isolated from other patches. While this results in a more efficient level of control than in the case of uncontrolled spatial dependence, this is not welfare maximizing : as a matter of

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<sup>2</sup>This can be viewed as an ecological version of inward and outward multilateral resistance terms ([Anderson and van Wincoop, 2003](#))

fact, the non cooperative equilibrium, while solving the spatial externality, does not leverage the spatial arbitrage opportunity provided by heterogenous costs of controling and biological productivities. When fencing displays (unequal) exclusionary and trap effects, best response functions are non monotonous. In this case, increasing fencing is not always optimal, and the Nash equilibrium results in suboptimal fencing, although closer to the optimal solution.

## 2 Related literature

There is a vast literature that investigates the optimal control, eradication and detection of invasive species (see [Epanchin-Niell \(2017\)](#) for a review of the economics of prevention, detection and control of invasive species through space). A much scarcer one looks at the spatial nature of the management of public bads and/or invasive species. These literature can be classified into 3 strands : trade, economic epidemiology and resource economics with different types of approaches to connectivity, space, and population dynamics.

Approaches from the trade literature consider the trade policy tools to avoid the introduction of alien invasive species. For example, [Olson and Roy \(2010\)](#) study the optimal use of sanitary and phytosanitary standards to prevent the introduction of pests through international trade. As pest and disease grow and spread over time their introduction has to be prevented. In a dynamic model, with non linear costs of trade restrictions, they investigate when full protection is efficient, and how prevention and control efforts need to be balanced.

The economic epidemiology literature uses different versions of the Susceptible Infected Recovered model ([Kermick and McKendrick, 1927](#)), where the evolution of each subpopulation forms a system of ordinary differential equations depending on epidemiological parameters, such as the infection or recovery rate. Such models have been refined to encompass more compartments of the subpopulation, including spatial approaches (for the spread of crop disease using a mean-field approximation, see ([Forster and Gilligan, 2007](#))), or age groups to guide policy during the COVID 19 pandemic ([Gollier, 2020; Acemoglu et al., 2021](#)). In these models, different rates of spread among subpopulations are possible and can be accomplished with differentiated lockdown policies. Notably, [Fenichel \(2013\)](#) studies the impact of social distancing and the impact of undifferentiated policies and include an endogenous component to the transmission rate, dependent on age specific characteristics and utility maximizing behavior, thus paving the way to analyze the endogeneity of disease spread and the role of economic incentives.

In the invasive species literature, early approaches such as [Huffaker et al. \(1992\)](#), [Bhat et al. \(1996\)](#) analyze various management regimes (cooperative, iso-

lated, and coordinated) to deal with the presence of beavers on private land. Using a framework stemming from metapopulation theory, they describe movement as a density dependent process, where relative densities dictate migration (an adaptation of Fick's Law of diffusion), which is, funny enough, an adaptation of Stenseth's "social fence" hypothesis [Stenseth \(1988\)](#). Optimal stock management needs to account for the migratory effects associated with population levels. With this analysis, [Huffaker et al. \(1992\)](#) and [Bhat et al. \(1996\)](#) limit themselves to two patches, for analytical and computational tractability. In this framework, fences are not really described, although dispersal is an endogenous process. A different approach, viewing space as a continuum, has considered options to halt the progression of an invasive species, using barrier zones, to ultimately slow the rate of spread [Sharov and Liebhold \(1998\)](#). While theoretically appealing, this approach may not be suited for operational concerns, whereby optimization on a continuum space is difficult, especially in various directions.

In the wake of [Brown and Roughgarden \(1997\)](#), [Bulte and van Kooten \(1999\)](#), [Sanchirico and Wilen \(1999\)](#) numerous models with spatially explicit metapopulation dynamics have been introduced, and soon became applied to the management of spatially distributed pests. For example, [Blackwood et al. \(2010\)](#) develop a linear quadratic framework to study the control of an invasive plant species. Taking advantage of the stock independent nature of dispersion patterns and of the linear quadratic structure, the authors solve the control and prevention problem at a large spatial scale. In more recent work, [Costello et al. \(2017\)](#) develop a large scale model of public goods, characterized by exogenous dispersal, stock-independent, and analyze the potential for eradication in a connected landscape. In doing so, they analyze the effects of varying connectivity parameters, without acknowledging for the potentially endogenous nature of dispersal. A wealth of papers, in the wake of [Sanchirico and Wilen \(1999\)](#), several papers ([Albers et al., 2010](#); [Ambec and Desquillet, 2012](#)) have investigated the use of policies to halt the spread of invasive species, including mandatory refuges, albeit uniform. While these articles view dispersal as a characteristic that can be influenced, they do not consider the optimal management, or lack thereof, of dispersal. Several article acknowledge the endogeneity of dispersal, such as [Janmaat \(2005\)](#), who highlights the role of dispersal in a fishery, and other parameters, to assess the extent of the tragedy of the commons. Interestingly, in that article, Janmaat states that "*until 'fences' are available to contain the 'wandering' offspring, management zones would have to be large. This would minimize the spillover, bringing the incentives of the 'owner' into line with maximizing the total return generated by the resource*". [Horan et al. \(2008\)](#) study conservation payments for various risk reducing ecological investments can be used to affect wildlife conservation and disease risk. In this article, they study how payments for ecosystem services affect habitat provision and connec-

tivity for the Andean deer, to protect them from disease carried by livestock. The analysis focuses on the temporal dynamics of the number of patches in different ecological states, adopting an SIR-like structure (i.e. share of states occupied by susceptible livestock or wildlife etc) from [McCallum and Dobson \(2002\)](#). The article does not study geographic, spatial patterns of habitat provision, but studies the provision of habitat in depth, and acknowledges the endogenous nature of habitat connectivity. In a more recent article, [Epanchin-Niell and Wilen \(2012\)](#) study the optimal management of an invasive species on a gridded landscape where species dispersal follows a cellular automaton : habitat patches are either occupied or not, and spread can be stopped using containment. The main idea of the present article resembles the approach in [Epanchin-Niell and Wilen \(2012\)](#), but explicitly considers the dynamics of species, and extends the approach to non cooperative settings. Finally, [Bode et al. \(2013\)](#) study the optimal use of interior fences (e.g. fraction the landscape into disconnected, equally sized patches) to reduce the costs of control of an invasive alien species on an island. While this approach is similar to the one developed in this article, it does not feature explicit spatial dynamics and ecological networks. In the current article, I build on these frameworks by using a discretized, raster-type landscape, with metapopulation dispersal across patches. Instead of analyzing how policies should adapt to dispersal, and I analyze how policies can shape dispersal and the decentralized, non cooperative equilibrium resulting from control and fencing decisions.

### **3 A dynamic spatial model of renewable bads management : fencing and controlling**

This model is adapted from [Costello et al. \(2017\)](#). It conserves the main features and includes an endogenous determination of landscape connectivity. For this version, I simplify the set-up to two players to investigate the value of connectivity.

#### **1 Spatial ecology**

Assume 2 patches indexed  $i \in \{A, B\}$  with a renewable resource. In a given period, the resource stock  $X_{it}$  is controlled by an amount  $h_{it}$ , and grows according to the remaining stock (or escapement), defined as  $e_{it} = X_{it} - h_{it}$ , such that the pre-dispersion population in patch  $i$  in  $t + 1$  is  $g_i(e_{it})$  such that  $g(0) = 0$ ,  $g'_i(e_{it}) \geq 0$ ,  $g''_i(e_{it}) \leq 0$ , allowing for local extinction and recolonization. Moreover, after the resource grows, it disperses through space (see fig. 2.A for a summary of the model timing). This is consistent with metapopulation models ([Sanchirico and Wilen, 1999](#); [Bulte and van Kooten, 1999](#)), although in a dis-

cretized timeframe (Costello et al., 2017). For now, I assume that dispersal depends exclusively on exogenous, immutable environmental characteristics. Density effects on dispersal rates are not considered in this model, to disentangle the effect of control decisions from fencing decisions on optimal management. Following Costello et al. (2017), dispersal rates from patch  $i$  to  $j$  is given by  $d_{ij} \in [0, 1]$ . As we study a closed system, when the resource does not disperse, it remains in patch  $i$  such that  $d_{ii} = 1 - d_{ij}$ . Therefore, in each period, a flow  $d_{ji}g_j(e_{jt})$  leaves patch  $i$  to patch  $j$  and a flow  $d_{jig_j}(e_{jt})$  leaves from patch  $j$  to patch  $i$ .

In conclusion, the patch specific population dynamics are given by :

$$\begin{aligned} X_{it+1} &= d_{ji}g_j(e_{jt}) + (1 - d_{ij}) g_i(e_{it}) \\ &= g_i(e_{it}) + (d_{ji}g_j(e_{jt}) - d_{ij}g_i(e_{it})) \end{aligned} \quad (3.1)$$

The first term denotes the population growth in patch  $i$ , and the second term in parenthesis denotes the net immigration from patch  $j$  to patch  $i$ . In terms of notations,  $\mathbf{D}$  refers to the matrix of dispersal rates.

## 2 Spatial economy

The presence of bads is costly in each patch via two channels, modeled as in Costello et al. (2017). First, the presence of bads implies property specific control expenditures. The larger the population, the lower the marginal cost of control: controlling the first unit at large population levels is cheaper than when the population is small. Marginal control costs feature a stock effect, where the marginal cost of control  $c_i(s)$  is decreasing with stock size,  $c'_i(s) < 0$ . The total cost of controlling down to residual stock  $e_{it}$  is  $\int_{e_{it}}^{X_{it}} c_i(s) ds$ .

Additionally, the presence of the residual stock causes heterogeneous marginal damages (for example, deer cause more damages to orchards and managed forests than to meadows)  $k_i(s)$ , which increase with stock size  $k'_i(s) > 0$ , resulting in convex damages. The total damages caused by the residual stock is  $\int_0^{e_{it}} k_i(s) ds$ .

The total cost in each patch  $i$  and period  $t$  is :

$$C_i(e_{it}, X_{it}) = \int_{e_{it}}^{X_{it}} c_i(s) ds + \int_0^{e_{it}} k_i(s) ds \quad (3.2)$$

The patch-period specific cost depends on current patch specific decisions, as well as past decisions by other agents, which influence the stock of bad in patch  $i$  at the beginning of period  $t$ . Finally, for ease of notation, variables in bold font are in vector form, e.g.  $\mathbf{X}_t = (X_{At}, X_{Bt})$ .

## 4 The value of connectivity

In this section, I first illustrate the value of changing connectivity patterns, and how fences can change them. To do so, I solve for the social planner of the model following (Costello et al., 2017) and illustrate how the value function changes with connectivity parameters.

### 1 Optimal residual stock in a connected world without fences

Before introducing the optimal determination of  $f_{At}$  and  $f_{Bt}$ , I focus on the case where  $f_{At} = f_{Bt} = 0$ , to illustrate the effects of changing the connectivity patterns *ex-nihilo*. Following Costello et al. (2017), the social planner aims to minimize the aggregate intertemporal welfare in patches A and B. Her program is :

$$\begin{aligned} \min_{\{\mathbf{e}_t\}_{t=0}^{\infty}} & \sum_{t=0}^{\infty} \delta^t \left( \sum_i C_i(e_{it}, X_{it}) \right) \\ \forall i \in \{A, B\} : & \\ X_{it+1} &= g_i(e_{it}) + (d_{ij}g_j(e_{jt}) - d_{ij}g_i(e_{it})) \end{aligned} \quad (3.1)$$

The Bellman equation can be written as:

$$\begin{aligned} V(\mathbf{X}_t) &= \min_{\mathbf{e}_t} \left( \sum_i C_i(e_{it}, X_{it}) + \delta V(\mathbf{X}_{t+1}) \right) \\ &= \min_{\mathbf{e}_t} \left( \sum_i C_i(e_{it}, X_{it}) + \right. \\ &\quad \left. \delta V(g_A(e_{At}) + (d_{BA}g_B(e_{Bt}) - d_{AB}g_A(e_{At})); \right. \\ &\quad \left. g_B(e_{Bt}) + (d_{AB}g_A(e_{At}) - d_{BA}g_B(e_{Bt}))) \right) \end{aligned} \quad (3.2)$$

Following proposition 5 of Costello et al. (2017), the optimal residual stock is given by :

**Proposition 3.1.** *The sole owner optimal control strategy has residual stocks  $\bar{\mathbf{e}}_t > 0$  characterized as follows :*

$$k_i(e_{it}^*) = c_i(e_{it}^*) - \delta \sum_j c_j(x_{jt+1}) d_{ij} g'_j(e_{it}^*) \quad (3.3)$$

As long as  $k_i(0) - (1 - \delta(1 - d_{ij}g'_i(0))c_i(0) + \delta g'_i(0)d_{ij}c_j(0)) < 0$ , otherwise  $e_{it}^* = 0$ .

As shown in Costello et al. (2017), this defines a state-independent solution, where  $\bar{\mathbf{e}}_t$  does not depend on  $\mathbf{X}_t$  (a version of the proof is given in appendix). For

an interior solution, the current marginal damage must equal the marginal cost of control, net of the future costs of control imposed by controlling one more unit of the bad. However, if the marginal damages are sufficiently low, or the dynamic costs expected to rise sharply, then the optimal solution is eradication. As such, in a disconnected world, local eradication and interior solutions can coexist.

A key question is to what extent are optimal residual stocks changing with given connectivity patterns. Optimal residual stock adapts to changes in dispersal in non trivial ways. As the social planner aims at keeping dynamic marginal costs balanced across patches, she has to change her optimal residual stocks when dispersal changes to account for differences in marginal costs. First, consider a world with homogeneous marginal control costs (i.e. where the difference only comes from the stock level, but costs are identical for a given population level) and growth. Consider any level of dispersal from  $B$  to  $A$  and low levels of dispersal from  $A$  to  $B$ . An increase in dispersal from  $A$  to  $B$  mechanically reduces the population in the next period in  $A$ , thus giving room to control more and lower residual stock in  $A$ , to reduce the aggregate costs. This is possible as the population level remains substantial, thus keeping the marginal cost of control relatively low. For example, if 5% of a deer herd migrates to a neighboring patch (and 95% remains), the additional 1% dispersion allows to control more, as damages are reduced, and the size of the herd is still substantial enough, such that it is not difficult to cull the population by one more unit.

At larger levels of dispersal from  $A$  to  $B$ , an increase in dispersal has a different effect. As the level of pest is already low, the marginal control cost of the remaining units is large. Hence, while the dispersal lowers the future population, and potentially its cost, maintaining a given level of residual stock comes at a very expensive cost. To continue with the deer example, if dispersal increases from 90% to 95%, continuing to cull the population at the same level becomes very expensive, as it is difficult to find the remaining individuals. Hence, residual stock is reduced, to use the low marginal level cost and variation in  $B$  and avoid an overburden in  $A$ .

Second, consider the effect of a marginal increase in inward dispersion (i.e. change in  $d_{BA}$ ). At low levels of outward dispersion (e.g.  $d_{AB} = .1$ ), the population in  $A$  is already large. Any increase in the future population level in  $A$  comes at a substantial cost, and to maintain equal costs across the landscape, the social planner sends some of the bad back by reducing residual stock in  $A$ . Now, at larger levels of outward dispersal (e.g.  $d_{AB} = .7$ ), the same mechanism applies for low increases in ingoing dispersal  $d_{AB}$ . However, the response changes, as here, more pest flow from  $A$  to  $B$ . In doing so, the cost in  $B$  is increased : to reduce the aggregate cost, residual stock in  $A$  must decrease. Proposition 3.2

establishes these effects.

**Proposition 3.2.** *In the case where optimal residual stock is interior (i.e.  $\forall i e_{it}^* > 0$ ) :*

- $\frac{\partial e_{it}}{\partial d_{ij}}$  is non monotonous (decreasing and increasing)
- $\frac{\partial e_{it}}{\partial d_{ji}}$  can be non-monotonous, and when monotonous, can be increasing or decreasing depending on the level of  $d_{ji}$

Finally, these effect depend on the fact that different stocks have different costs. With heterogeneous linear marginal costs, residual stock react in a monotonous way to changes in dispersal to balance the change in aggregate costs. With homogeneous non-linear marginal costs, different levels of population cause different control costs, even though they are on the same curve. Absent some sort of heterogeneity, there is no change in optimal residual stock, as the dynamic marginal control costs are equal across patches, and heterogeneous levels may only arise from differences in marginal damages and growth patterns across patches. Finally, changes in connectivity patterns can break interior solutions and foster either eradication, or residual stock is limited by the stock and no control is undertaken (i.e.  $e_{it} = X_{it}$ ). In this case, the optimal solution in proposition 3.1 no longer holds and the optimal residual population depends on the population in  $t$ ,  $X_{it}$ . In the case of source-sink dynamics, i.e. when patch  $A$  retains a lot of its population, while the population from patch  $B$  leaves almost integrally to  $A$ , control is not undertaken in  $B$  : the marginal cost of control is too important. More control is undertaken in  $A$ , and the aggregate stock decreases.

## 2 Analytical value of marginal dispersal changes

The value function, in turn, can be rewritten taking into account the dispersal matrix  $\mathbf{D}$  as :

$$V(\mathbf{X}_0, \mathbf{D}) = \sum_{i \in \{A, B\}} \left( \int_0^{e_{it}^*} k_i(s) ds + \int_{e_{it}^*}^{X_{it}} c_i(s) \right) + \delta V(X_1^*)$$

Using this formulation, one can identify the effect of a change in connectivity. For example, the value of a change in connectivity (through a change in dispersal from  $A$  to  $B$ , see Appendix) :

$$\begin{aligned} \frac{\partial V(\mathbf{X}_0, \mathbf{D})}{\partial d_{AB}} = & g'_A(e_{At}^*)(c_B(X_{At+1}^*) - c_A(X_{Bt+1}^*)) + \\ & \frac{\partial e_{At}^*}{\partial d_{AB}} (g'_A(e_{At}^*)(c_A(X_{At+1}^*)(1 - d_{AB}) + d_{AB}c_B(X_{Bt+1}^*)) + \\ & \frac{\partial e_{Bt}^*}{\partial d_{AB}} (g'_B(e_{Bt}^*)(c_A(X_{At+1}^*)d_{BA} + (1 - d_{BA})c_B(X_{Bt+1}^*)) \end{aligned} \quad (3.4)$$

Welfare changes through direct and indirect effects of changes in dispersal patterns. The first line measures the direct effect of a change in dispersal from  $A$  to  $B$ , as the stock grows in  $A$  and travels from  $A$  to  $B$ , thus incurring marginal control costs in  $B$  rather than in  $A$ . The second and third lines measure the adaptation of the optimal residual stock to changes in dispersal. As highlighted above, the effect of a change in dispersal has ambiguous effects on optimal residual stock. The effect of a change in dispersal on welfare depends on how optimal residual stock change in both patches. The changes in optimal residual stock cause a change in growths in each patch. In patch  $A$ , the marginal unit of bad  $g' A(e_{At}^*)$  remains for  $(1 - d_{AB})\%$  in patch  $A$  and causes control costs  $c_A(X_{At+1}^*)$ , while  $d_{AB}\%$  moves to  $B$  and causes control costs  $c_B(X_{Bt+1}^*)$  there.

Depending on the initial dispersal pattern  $\mathbf{D}$ , changes in connectivity patterns have intricate effects, as the reaction of optimal escapement is non-monotonous. Welfare changes with connectivity in the presence of heterogeneous, stock-dependent marginal costs of control, as spatial arbitrage opportunities exist. As the impact of marginal changes in connectivity patterns can be both positive and negative, optimal connectivity exists, depending on the nature of marginal damages, marginal costs and growth. Using these variations, one can compute the global effect of a change in connectivity patterns. However, this is beyond analytical tractability. Hence, I move onto a numerical illustration.

### 3 Numerical illustration

I specify the problem using functional forms to illustrate the value of connectivity. Table 3.1 lists the functional forms as well as the associated parameterization. I use a linear quadratic damage function, an inverse marginal cost function, and a logarithmic growth function, with calibrated parameters, to ensure the emergence of an interior solution. Figure ?? illustrates these functions.

Function		$A$	$B$
Marginal Cost	$mc_i(x) = \frac{\gamma_i}{1+k_i x_i}$	$\gamma_A = 10$ $k_A = 4$	$\gamma_B = 10$ $k_B = 4$
Marginal Damage	$md_i(x) = md_0 + md_1 x_i^2$	$md_{1A} = 2$ $md_{0A} = 2$	$md_{1B} = 2$ $md_{0B} = 2$
Growth Function	$g_i(x) = a_i \times \log(1 + b_i x)$	$a_A = 0.95$ $b_A = 1$	$a_B = 0.95$ $b_B = 1$
Initial Stock		$X_{A0} = 1$	$X_{B0} = 1$
Planning Parameters		$\delta = 0.95$	
Planning Parameters		$T = 50$	

Table 3.1: Parameter Definitions for model illustration

Using the implicit solution defined in proposition 3.1, I solve the model over  $T = 50$  periods, using the full range of  $d_{AB}$  and  $d_{BA}$ .

### 3.1 Optimal residual stock and dispersal

Figure 3.4a displays the optimal levels of residual stock and the subsequent population levels through time, across quartiles of the value function. Results are symmetric. For lower values of the value function, optimal residual stock is relatively low in both patches, and increases as the value function increases gradually. The spread between residual stocks narrows as dispersal parameters become more symmetric. The dispersal patterns allow for more control in the case of sink-source dynamics, thus lowering the value function.

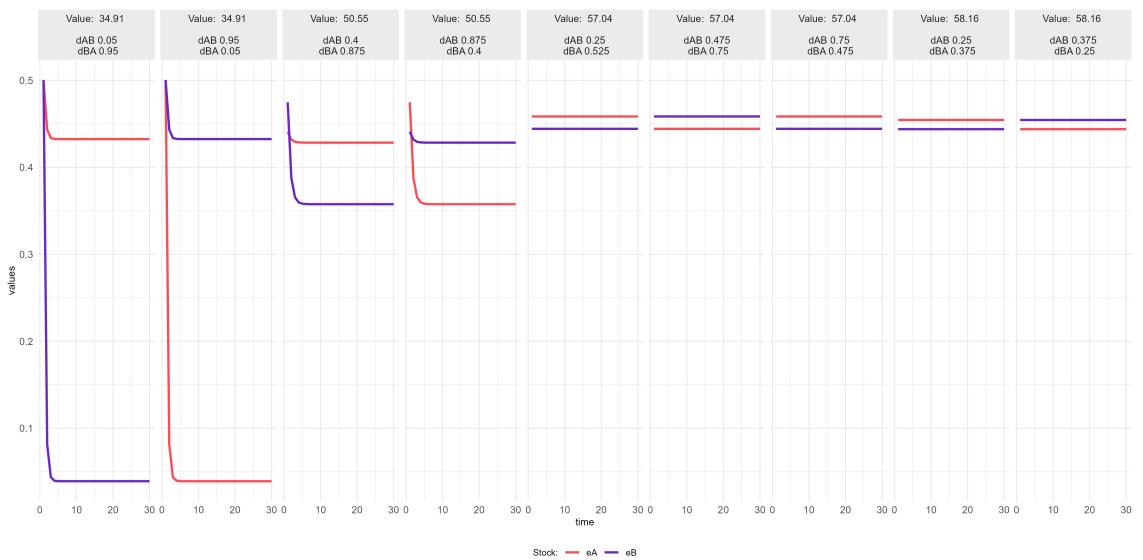


Figure 3.1: Optimal stock and residual stock levels across patches for quartiles of the value function

Figure 2.Ca shows the variations in residual stock for interior and corner solutions. For low values of dispersal from  $A$  to  $B$ , residual stock in  $A$  decreases, but increases after  $d_{AB} > .5$ . Variations depend on the relative magnitude of  $d_{AB}$  and  $d_{BA}$ , and display the non linear trends highlighted in proposition 3.2. Finally, figure 2.Cb shows the evolution of optimal residual stock, constrained by low stock levels in respective patches.

### 3.2 Value and connectivity

The mechanisms highlighted above are illustrated in the surface map of the value function across  $d_{AB}$  and  $d_{BA}$ . For sink-source dynamics (top right and bottom left corners), the dispersal patterns allow to control more of the population, resulting in lower population through time and lower damages. As dispersal patterns are

more symmetric, the optimal intertemporal costs tend to increase. Ultimately, although the numerical values only serve an illustrative purpose, they show a stark result: if connectivity is manageable at limited costs, leveraging spatial arbitrage opportunities can increase welfare by almost 40%.

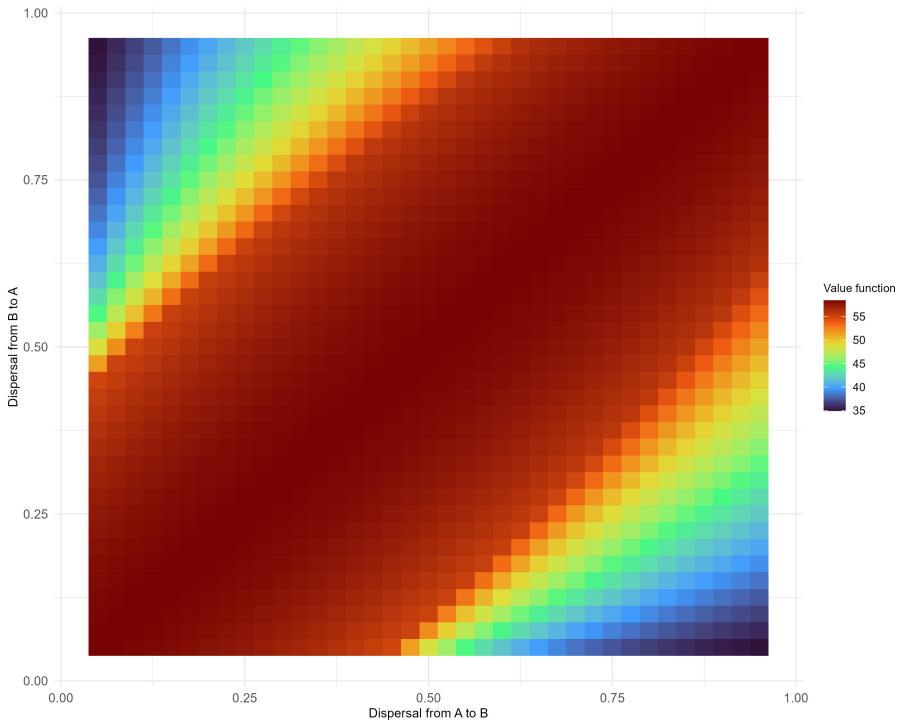


Figure 3.2: Intertemporal costs of mobile public bad depending on landscape connectivity patterns

## 5 Introducing fences

### 1 Definition and properties

As there is value to manage connectivity, connectivity measures are likely being implemented, unless they are prohibitively costly. In this part of the model, dispersal rates between patches depends on directional fencing expenditures in both patches, with  $d_{ijt+1} \equiv d_{ijt+1}(f_{it}, f_{jt})$ , where  $f_{it}$  measures the amount of fencing in patch  $i$  in direction of patch  $j$ , as a percentage rate of maximal fencing, such that  $F = \{f_{it} + f_{jt} \leq 2\}$ . The rate of inward dispersion of invasive species from  $i$  to  $j$ ,  $d_{ijt+1}(f_{it}, f_{jt})$  decreases with  $f_{jt}$ . I call this the "exclusionary effect": fences keep nuisances out of  $j$ . When fencing in  $i$  at  $f_{it}$ , the outward dispersion of invasive species from  $i$  to  $j$  decreases as well, as species get trapped in  $i$ . This effect is the "trap effect": fences trap the nuisance in. However, in most cases of exclusionary fencing, the exclusionary effect dominates the trap effect, allowing for trapped animals to escape. Fencing reduces the inward dispersion from  $i$  to  $j$  at a decreasing rate, whether it is undertaken in patch  $i$  or  $j$ . The rate of patch re-

tention  $d_{iit+1}$  is the remainder after dispersions from  $i$  to  $j$ . When no fencing is undertaken, the dispersal rate remains at a rate determined by immutable environmental factors (landscape discontinuities, mountains, terrain ruggedness etc), such that  $d_{ijt+1}(0, 0) = m_{ij}$ . When the maximal amount of fencing is undertaken, dispersal drops to  $n_{ij}$ . Dispersal rates are ultimately affected by immutable environmental factors (landscape discontinuities such as roads, rivers, moutains; altitude and terrain ruggedness etc).

$$\begin{aligned}
 d_{ijt+1} : F &\rightarrow [n_{ij}, m_{ij}] \subset [0, 1] \\
 \underbrace{\frac{\partial d_{ijt+1}}{\partial f_{it}}}_{\text{Exclusionary effect}} &\leq \underbrace{\frac{\partial d_{ijt+1}}{\partial f_{it}}}_{\text{Trap effect}} \leq 0 \\
 d_{ijt+1}(f_{it}, f_{jt}) + d_{iit+1} &= 1
 \end{aligned} \tag{3.1}$$

As such, fences have public good features: whether  $A$  or  $B$  fences, both the inbound and outbound dispersal are affected, while only pf them pays the price.

In practice, for numerical simulations, I adapt dispersal rates from metapopulation theory using a negative exponential dispersal kernel (Hanski et al., 2000; Moilanen, 2004). Fencing acts as increasing the distance between patches, and conversely, as reducing the mean dispersal distance of a species in a given patch :

$$d_{ijt+1}(f_{it}, f_{jt}) = \exp(-\theta(f_{j|t} + \beta_i f_{i|t}) \times (m_{ij} - n_{ij}) + n_{ij} \tag{3.2}$$

Where  $\theta$  is a scaling parameter, and  $\beta_i$  measures the relative effect of fences in  $i$  compared to fences in  $j$  to reduce  $d_{ijt+1}$ . Figure 3.3 illustrates dispersal between  $A$  and  $B$  with asymmetric bounds to dispersal (i.e.  $m_{ij} \neq m_{ji}$  and  $n_{ij} \neq n_{ji}$ ).

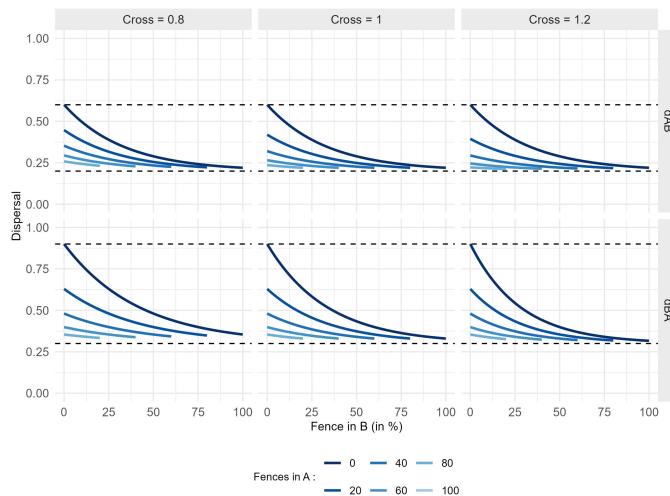


Figure 3.3: Dispersal depending on fencing decision in  $A$  and  $B$  with asymmetric bounds and cross efficiencies

On the left panel,  $\beta_A = .8$  describes a situation where the trap effect dominates, while on the right panel,  $\beta_A = 1.2$  displays a situation where the exclusionary effect dominates

Fences change dispersal in a specific way, as they only diminish connectivity between patches, and increase self retention. In the case where patches have the same bounds to dispersal ( $n_{AB} = n_{BA}$  and  $m_{AB} = m_{BA}$ ), fencing is not in the interest of the social planner : dispersal remains symmetric, and the value function does not vary along the symmetry axis between  $d_{AB}$  and  $d_{BA}$ . Indeed, when fencing retains as much population in as it does keep out, the net effect on the next period population is null. As fences come to a certain cost, it always outweighs inexistent benefits. However, when bounds to dispersal are asymmetric, fencing can have a positive effect on welfare. As dispersal is decreased to asymmetric inferior bounds, the population stock across patches changes asymmetrically as well. In doing so, one can leverage the spatial arbitrage opportunity associated with asymmetric dispersal and non-homogenous nonlinear costs, as well as different marginal damages.

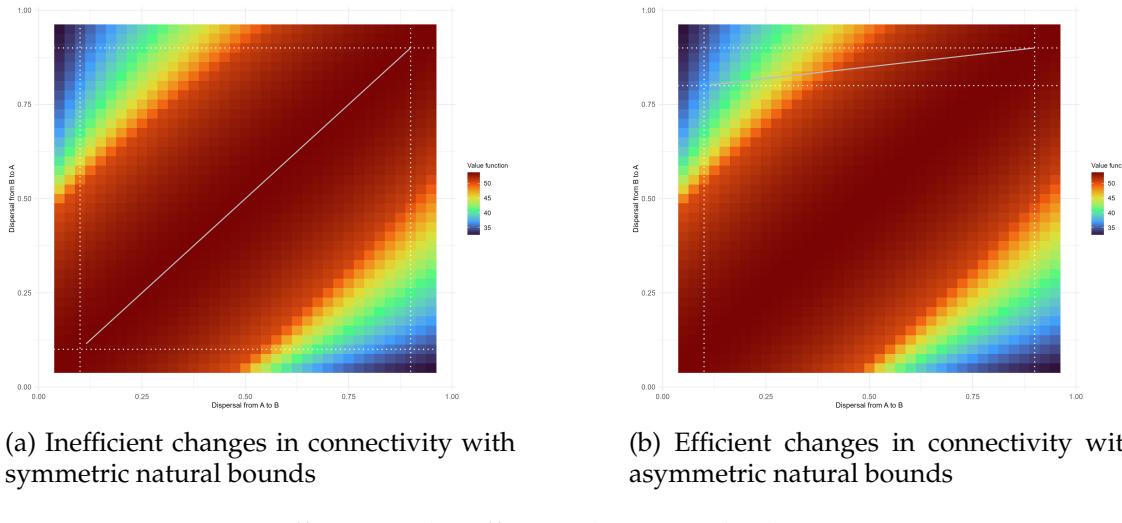


Figure 3.4: Efficient and inefficient changes in landscape connectivity

## 2 Spatial ecology and economy with fences

With fences, the spatial ecology of the problem is modified as follows, with  $d_{ijt+1}(f_{it}, f_{jt})$  defined as in equation 3.1:

$$\begin{aligned} X_{it+1} &= d_{ijt+1}(f_{it}, f_{jt})g_j(e_{jt}) + (1 - d_{ijt+1}(f_{it}, f_{jt}))g_i(e_{it}) \\ &= g_i(e_{it}) + (d_{ijt+1}(f_{it}, f_{jt})g_j(e_{jt}) - d_{ij}(f_{it}, f_{jt})g_i(e_{it})) \end{aligned} \quad (3.3)$$

Fences are expressed as a percentage of the maximal rate of fencing doable. Anecdotal evidence suggests that fencing costs increase in a convex way: marginally reducing the passage of species or viruses can be done at a low costs, while more efficient devices can reach large costs<sup>3</sup>. For the sake of simplicity, I nonetheless

<sup>3</sup>Methods range from scent and taste-based repellents, that need to be reapplied frequently

restrict the analysis to linear costs, such that the current payoff is modified. The total cost in each patch  $i$  and period  $t$  is :

$$C_i(e_{it}, X_{it}, f_{it}^1, \dots, f_{it}) = \int_{e_{it}}^{X_{it}} c_i(s) ds + \int_0^{e_{it}} k_i(s) ds + \kappa_i f_{it} \quad (3.4)$$

## 6 A world with endogenous connectivity and population

### 1 Socially optimal management: conditions for interior solutions

When dispersal can be managed (i.e.  $n_{AB} \neq m_{AB}$  and/or  $n_{BA} \neq m_{AB}$ ), the sole owner decides both the levels of fencing and residual stock. Proposition 3.3 establishes the conditions under which both interior fencing and residual stock exist:

**Proposition 3.3.** *Interior optimal residual stock in each patch  $i$  is such that :*

$$k_i(e_{it}) = c_i(e_{it}) - \delta g'_i(e_{it}) [c_i(X_{it+1}) + d_{ijt+1}(f_{it}, f_{it}) c_j(X_{jt+1}) - c_i(X_{it+1})] \quad (3.1)$$

*And optimal fencing in patch  $i$  towards patch  $j$  is :*

$$\kappa_i = \delta \left( \frac{\partial d_{ij+1}}{\partial f_{it}} g_i(e_{it}) - \frac{\partial d_{j�+1}}{\partial f_{it}} g_j(e_{jt}) \right) (c_i(X_{it+1}) - c_j(X_{jt+1})) \quad (3.2)$$

*Additionally, interior fencing and control are state-independent i.e. solutions do not depend on  $\mathbf{X}_t$  (see proof in appendix E.1).*

The optimal residual stock in patch  $i$  is such that the current marginal damage caused by letting the marginal unit matches the corresponding control cost, mitigated by the discounted global cost effect, as in [Costello et al. \(2017\)](#) (refered to as the *dynamic marginal cost effect*). When a marginal unit of bad is controlled, marginal damage  $k_i(e_{it})$  are not incurred in patch  $i$ . This marginal damage has to equal the current period cost of controling  $c_i(e_{it})$ , and the discounted next period cost. A marginal unit of bad will grow according to  $g'_i(e_{it})$ , and disperse through space. A portion  $d_{iit+1} = 1 - \sum_{j \neq i} d_{ijt+1}(f_{it}, f_{it})$  remains in the patch (and sets the marginal cost of control at  $c_i(X_{it+1})$ ), while a fraction goes in each connected patch  $j$ , incurring a decrease in marginal control costs of  $c_j(X_{jt+1})$ . The extent of

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and cost 15-50\$ per gallon, to electric fencing (at 3-5\$ a foot), and landscape modifications such as gullies and dams (ranging from 500 to 5,000\$ per work), and finally, regular human presence. In the case of viruses, strategies range from wearing surgical masks to partial and complete lockdowns, with different economic costs. [Gollier \(2020\)](#); [Acemoglu et al. \(2021\)](#) analyze the costs of different lockdown strategies with multigroup SIR models, in the context of COVID 19. They focus on age-specific disease spread rates, which is akin to considering spatially differentiated spread rates. They show that efficient, targeted lockdown strategies are paramount as their costs are convex.

control thus depends on the current marginal damages and costs, and the spatial dynamic component. If dispersal to neighbors is *naturally* large, and the marginal cost of control tends to be lower in these patches, residual stock increases, leveraging a spatial arbitrage opportunity.

Interior fencing is a novel result. In a given patch, the sole owner fences such that the current marginal cost of fencing equals the discounted marginal benefits of fencing. These benefits emerge from the use of a spatial arbitrage opportunity. Positive fencing occurs in  $i$  if the *exclusionary* effect of fencing (i.e. the marginal population that remains in  $j$  following an increase in fencing in  $i$ ) outweighs the *trap* effect (i.e. the marginal population that remains in  $i$  following an increase in fencing in  $i$ ), and the marginal cost of control are larger in  $i$  than in  $j$ . Positive fencing in  $i$  can also emerge if the *trap* effect dominates the *exclusionary*, but control costs are larger in  $j$  than in  $i$ . To further characterize the optimal management, I restrict the analysis to the case of constant marginal costs of control. In the next subsections, I disentangle the effects of the trap and exclusion effects with constant marginal costs of control.

### 1.1 No fencing in the absence of spatial arbitrage opportunity

The spatial arbitrage opportunity arises from the difference in control costs across space and for different stock levels. In that case, the absence of control cost heterogeneity implies no fencing : redirecting the resource flow has no interest, since there is no additional cost reduction to be expected. Although patches are connected, there is no heterogeneity to leverage. As a consequence, the optimal control rule is independent of dispersal. In this case, the discounted future cost of controlling the increased stock in patch  $i$  equal the current costs net of damages. Moreover, the optimal control does not depend on spatial dispersal, as the cost of control are homogenous, and depends only on patch specific characteristics. In this specific homogeneous linear case, the equilibrium collapses to the disconnected optimal control strategy defined in proposition 3.4.

**Proposition 3.4.** *With linear homogeneous control costs (e.g.  $\forall i, c_i(s) = c$ ), or no spatial dispersal (i.e.  $d_{ii} = 0$  and  $d_{jj} = 0$ ), optimal management consists in no fencing  $\forall i, j, f_{it} = 0$  and optimal residual stock is implicitly defined by:*

$$c\delta g'_i(e_{it}) = c - k_i(e_{it})$$

*See proof in appendix E.2*

## 1.2 Optimal management with heterogeneous costs and exclusionary fencing

Assume control costs are heterogeneous, such that  $c_A > c_B$ . In this case, there is a potential to levy a spatial arbitrage opportunity : if the stock were more directed towards patch  $B$ , larger levels of control could be undertaken with the same budget (or equivalently, the same amount of aggregate control could be undertaken at a lower cost). In this example, I assume fencing only has an exclusionary effect. In real life, exclusionary fencing is a common practice in conservation. For example, the Kilauea Point National Wildlife Refuge in Hawaii has implemented a predator exclusion fence to protect native seabirds from mammalian predators<sup>4</sup>. I focus on the case where exclusionary fences allow the population of predators to escape<sup>5</sup>.

In patch  $A$ , if fencing only has an *exclusionary effect* and no *trap effect*, fencing keeps the stock from  $B$  out, while allowing the stock from  $A$  to escape. Upon fencing, the sole owner gains clear marginal benefits, as the stock that used to flow from  $B$  to  $A$  no longer does, and the stock can still flow from  $A$  to  $B$ , reducing the total cost. In this case, the sole owner has an interest in reshaping how the stock moves through space, and thus, to reshape the spatial externality, such that resources flow to patch  $B$ .

**Proposition 3.5.** *With heterogeneous, constant marginal cost of fencing such that  $c_A > c_B$ ,  $[n_{ij}, m_{ij}] \subset ]0, 1[$  and fencing only displays an exclusionary effect i.e. :*

$$d_{ijt+1}(f_{it}, f_{jt}) = d_{ijt+1}(f_{jt}) \\ \frac{\partial d_{ijt+1}}{\partial f_{jt}} < 0$$

*The optimal allocation is :*

$$\kappa_A = \delta(c_A - c_B) \left| \frac{\partial d_{BA_{t+1}}}{\partial f_{At}}(f_{At}^*, 0) \right| \quad (3.3)$$

$$f_{Bt} = 0 \quad (3.4)$$

$$k(e_{At}) = c_A - \delta g'_A(e_{At})(c_A(1 - d_{AB_{t+1}}(0)) + c_B d_{AB_{t+1}}(0))) \quad (3.5)$$

$$k(e_{Bt}) = c_B - \delta g'_B(e_{Bt})(c_B(1 - d_{BA_{t+1}}(f_{At}^*)) + c_A d_{BA_{t+1}}(f_{At}^*)) \quad (3.6)$$

Proposition 3.5 shows that when spatial arbitrage opportunities are not exhaustible, the sole owner fences only in  $A$  to avoid inward dispersal from  $B$ ,

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<sup>4</sup>The 11,200 foot fence protects 168 hectares of wildlfe habitat and even includes underground skirt and curved hood to avoid climbing over or digging under, see <https://www.fws.gov/story/2023-08/pacifics-largest-predator-exclusion-fence>

<sup>5</sup>In this case, the fencing technology can be seen as akin to an electrical resistance

while it does not change how much  $B$  receives inward dispersion, as any dispersion from  $A$  to  $B$  is welfare improving. The response of optimal residual stock to changes in dispersal depends on the second order conditions of the problem<sup>6</sup>.

Assume now that fencing only has a trap effect. For example, small scale fencing has long been used in the US to manage feral pigs populations, where animals get entrapped, but more can come in<sup>7</sup>. In patch  $A$ , if fencing only has a *trap effect* and no *exclusionary effect*, fences keep the stock inside of  $A$ , while they do not reduce the inward dispersion from patch  $B$ . As costs of control are smaller in  $B$  than in  $A$ , a sole owner would benefit from keeping the population in  $B$  where it is cheaper to control, and let the population from  $A$  get trapped in  $B$ . The mechanism described here is *in fine* symmetrical to the *exclusionary case*, but fences are located in  $B$ .

### 1.3 Optimal management when fencing displays exclusionary and trap effects

In most cases, fences has a both an *exclusionary* and *trap effect*, e.g. fencing reduces the inward dispersion from other patches to a given patch  $A$ , and reduces the outward population dispersion from patch  $A$  to other patches. Following equation 3.2, two effects are at play. First, fencing still results from a spatial arbitrage opportunity, from the spatial heterogeneity in marginal control costs. Second, the interplay between the *exclusionary effect* and the *trap effect* is key for fencing to be welfare improving, and biological productivity becomes important to decide where to locate the fences. In the case of patch  $A$ , optimal fencing arises if more of the pest population is kept out than in, while optimal fencing in  $B$  arises if more of the population is kept in than out.

**Proposition 3.6.** *When fencing has both an exclusionary effect and trap effect, with (i) heterogeneous costs of control, (ii) homogeneous cost of fencing, (iii) identical dispersal and (iv) the exclusionary effect dominates the trap effect, fencing occurs in patch  $i$  if:*

1.  $c_i > c_j$  and the exclusionary effect dominates the trap effect for some values of  $e_{it}, e_{jt}, f_{it}$ :

$$\frac{\kappa}{c_i - c_j} + \left| \frac{\partial d_{ijt+1}}{\partial f_{it}} \right| g_i(e_{it}) < \left| \frac{\partial d_{j�+1}}{\partial f_{it}} \right| g_j(e_{jt}) \quad (3.8)$$

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<sup>6</sup>As a matter of fact :

$$\frac{\partial e_{Bt}}{\partial f_{At}} = \frac{\kappa_A}{SOC_B} \delta g'(e_{it}) \quad (3.7)$$

Where  $SOC_B = k'_B(e_{Bt}) + \delta g''_B(e_{Bt})((1 - d_{BAt+1}(f_{At}^*))c_B + d_{BAt+1}(f_{At}^*)c_A)$  is the second order condition of the problem with respect to  $e_{Bt}$ . As I do not fully analyze the second order conditions, it is impossible to substantiate claims further. However, notice that is negative when the increase in the marginal damage is lower than the increase in dynamic costs, and positive otherwise. As conditions for a global minimum differ with multivariate objective functions, this is a possibility to investigate further

<sup>7</sup>see <https://www.aphis.usda.gov/sites/default/files/managing-feral-pigs.pdf>

2.  $c_i < c_j$  and the trap effect dominates the exclusionary effect for some values of  $e_{it}, e_{jt}, f_{it}$ :

$$\frac{\kappa}{c_j - c_i} + \left| \frac{\partial d_{ijt+1}}{\partial f_{it}} \right| g_i(e_{it}) > \left| \frac{\partial d_{j�+1}}{\partial f_{it}} \right| g_j(e_{jt}) \quad (3.9)$$

3. If fencing occurs in patch  $i$ , it does not occur in patch  $j$

*See proof in appendix E.4*

Proposition 3.6 states that fencing in patches  $A$  depends on control cost, biological productivity heterogeneity, and the relative effects of fencing. When fences keep as much out as they keep in, biological productivity must be such that benefits from fencing still emerge due to initially large population levels and heterogeneous constant marginal costs of control. Contrary to the case of variable marginal control costs, heterogeneity in the bounds of dispersal, and thus on the effects of fences, does not provide any spatial arbitrage opportunity alone.

With heterogeneous costs of control, this result shows that fencing is optimal (at least temporarily and partially) to isolate a patch with a large growth : this result concurs with [Epanchin-Niell and Wilen \(2012\)](#) who find isolation to be a welfare improving strategy (in a different modeling system, with spatially explicit cellular automata). In real life, temporary quarantine is applied at small scales (for example within a cattle) and larger scales (such as the country scale during epidemics such as the foot and mouth disease in 2001 in the UK). When fences play more of an exclusionary than trap effect, a naive argument would call for fencing in  $A$  as long as the rate at which fencing decreases inward dispersion from  $B$  is larger than the rate at which fencing increases self retention in  $B$ . However, population levels matter. Indeed, if population growth is sufficiently high in  $A$ , the self retained population in  $A$  may be very large, even though the rate of self retention increases at a slower pace than the rate of inward dispersion from  $B$  decreases. Finally, with homogeneous growth, fencing in  $A$  is incompatible with fencing in  $B$ .

To conclude, in the presence of spatial heterogeneity in control costs, optimal management leverages a spatial arbitrage opportunity. Dispersal rates are modified to take advantage and redirect pest populations where they are least costly. However, if in a patch, biological growth and control costs are larger than in the other patch, fencing may not be optimal, as the retained population causes additional burden as it tries to avoid more population inward dispersion from the cheap, low growth patch.

## 2 Non cooperative equilibrium

I now turn to the analysis of the non cooperative equilibrium, where each patch owner determines their optimal level of control and fences in each period. Two effects are at play. First, the spatial externality is not internalized in a non cooperative equilibrium : the costs borne by neighboring patches are not internalized, hence resulting in under control, as highlighted in [Costello et al. \(2017\)](#). Second, the equilibrium provision of fences will depend on their properties, whether they are only exclusionary or also display a trap effect. Fences allow to resolve the spatial dependency on other players, i.e. they solve the spatial externality. However, they also feature public good properties, as fencing in  $A$  not only reduces the outward dispersion from  $B$  to  $A$ , but also the inward dispersion from  $A$  to  $B$ . Each patch owner in  $A$  and  $B$  aims to minimize the present value cost subject to choices in residual stock and fences:

$$V_{it}(\mathbf{X}_t) = \min_{e_{it}, f_{it}} \left( \int_0^{e_{it}} k_i(s) ds + \int_{e_{it}}^{X_{it}} +\kappa_i f_{it} + \delta V_{it+1}(\mathbf{X}_{t+1}) \right) \quad (3.10)$$

In what follows, I use Markov Perfect Nash Equilibrium as a solution concept. The residual stock and fencing rules from an MPNE if given information about the population levels in  $t$ , they are optimal rules for subsequent periods. In line with the previous part, I assume linear costs of control. In the case of an interior equilibrium, residual stock and fencing by each player is characterized by :

**Proposition 3.7.** *The interior equilibrium is characterized by residual stock and fencing levels in patch  $i$  given by :*

$$k_i(\bar{e}_{it}) = c_i(1 - \delta g'_i(\bar{e}_{it})(1 - d_{ijt+1}(\bar{f}_{jt}, \bar{f}_{it}))) \quad (3.11)$$

$$\kappa_i = \delta c_i \left( \frac{\partial d_{ijt+1}}{\partial \bar{f}_{it}} g_i(\bar{e}_{it}) - \frac{\partial d_{ijt+1}}{\partial \bar{f}_{jt}} g_j(\bar{e}_{jt}) \right) \quad (3.12)$$

*See proof in appendix F.1*

In this case, each landowner does not internalize the costs she's causing the other, hence this results in under residual stock in the case of interior solutions. Second, the fencing strategy of each owner only depends on their costs, and not on the cost differential. The optimal fencing strategy is determined such that the marginal cost of fencing ( $\kappa_i$ ) equals the discounted marginal benefits of fencing i.e. the cost of the marginal change in net dispersion flow following a change in fencing in  $A$ .

To gain further intuition, assume a fully homogeneous world : control costs and fencing costs are homogeneous ( $c_A = c_B = c$  and  $\kappa_A = \kappa_B = \kappa$ ), the effect of fencing on the outward dispersal flow are identical, and the effect of fencing

on the inward dispersal flow are identical (i.e.  $\frac{\partial d_{ABt+1}}{\partial f_{At}} = \frac{\partial d_{BAt+1}}{\partial f_{Bt}}$  and  $\frac{\partial d_{ABt+1}}{\partial f_{Bt}} = \frac{\partial d_{BAt+1}}{\partial f_{At}}$ ).

## 2.1 Homogeneous costs, growth and damages.

To gain intuition, assume fencing only displays an exclusionary effect i.e.  $\frac{\partial d_{ijt+1}}{\partial f_{it}} = 0$ . This example is in many ways simplifying (especially as marginal costs of control are assumed linear), but captures essential intuition. For example, during the COVID pandemic, from March to June 2020, the European Union issued **temporary restrictions** on non-essential travel *into* the EU, along with other states such as the **United States**. In this case, a race to the bottom in terms of connectivity arises, as fences do not feature public good properties. As each player builds more fences, it increases the share of pest remaining in the neighboring patch. In doing so, it increases the dynamic costs and damages inflicted on the neighbor. Every player has an interest in fencing up to the point where the cost of increasing fencing equals the avoided cost from decreasing the inward dispersion flow. No player has an interest to deviate from this strategy: if player  $A$  fences below the individual marginally efficient level, player  $B$  does not decrease her fences, and more population flows from  $B$  to  $A$ , resulting in lower costs and damages for  $B$ . Hence, the equilibrium is a situation where both players over-fence compared to the optimum and undercontrols.

In the limiting case where dispersal can be completely shut down (for example, if the marginal cost of fencing  $\kappa$  is low compared to damages) such that  $d_{ijt+1} = d_{jxt+1} = 0$ , individual residual stock is optimal, as shown in proposition 3.4. However, the fencing level is suboptimal.

**Proposition 3.8.** *With (i) constant homogeneous marginal cost of control, (ii) homogeneous costs of fencing, (iii) homogeneous growth and marginal damage and (iv) homogeneous exclusionary fencing, the non cooperative equilibrium is :*

$$k(\bar{e}_{it}) = c(1 - \delta g'(\bar{e}_{it})(1 - d_{ijt+1}(\bar{f}_{jt})) \quad (3.13)$$

$$\kappa = c \left| \frac{\partial d}{\partial f_i} \right| g_j(\bar{e}_{jt}) \quad (3.14)$$

*Under direct application of the first order conditions*

Now, assume fencing displays a both exclusionary and trap effects. Assume the exclusionary effect dominates the trap effect, such that  $\left| \frac{\partial d_{ijt+1}}{\partial f_{jt}} \right| > \left| \frac{\partial d_{ijt+1}}{\partial f_{it}} \right|$  and  $\frac{\partial d_{ijt+1}}{\partial f_{jt}} = \beta_j(f_{jt}) \frac{\partial d_{ijt+1}}{\partial f_{it}}$  with  $\beta_j(f_{jt}) \geq 1$ . In the case of constant marginal costs of control, [Costello et al. \(2017\)](#) show that the equilibrium residual stock in each patch increases with inward and outward dispersal rates. As the exclusionary effect dominates, increases in fencing in each patch decrease inward dispersal

more than outward dispersal. Additionally, residual stocks decreases. Hence, each player has an incentive to increase fencing to decrease the inward dispersal flow, and no interest in deviating, as the exclusionary effect dominates : upon deviation, residual stock in the neighboring patch increases, and the inward dispersal share increases, causing additional costs and damages. In the case of interior solutions, the non cooperative equilibrium results in suboptimal fencing, as fencing is undertaken in two patches. As a result, the interior non-cooperative equilibrium is inefficient.

**Proposition 3.9.** *When the exclusionary effect of fencing always dominates the trap effect, the decentralized equilibrium is given by :*

$$k(\bar{e}_{it}) = c(1 - \delta g'(\bar{e}_{it})(1 - d_{ij}(\bar{f}_{jt})) \quad (3.15)$$

$$\kappa_i = \delta c_i \left| \frac{\partial d_{ijt+1}}{\partial f_{it}} \right| (\beta_i(\bar{f}_{it})g_j(\bar{e}_{jt}) - g_i(\bar{e}_{it})) \quad (3.16)$$

Hence,  $\bar{f}_{it} > 0$ ,  $\bar{f}_{jt} > 0$  and  $\bar{e}_{it} \neq e_{it}^*$

If the exclusionary effect and the trap effect are identical and homogeneous across patches, in the decentralized equilibrium, no fencing is undertaken, as it reduces the individual welfare : upon fencing, each player incurs cost  $\kappa$  while not changing the inbound or outbound rate of dispersal. In this case, the equilibrium is identical to the equilibrium extensively analyzed in ([Costello et al., 2017](#)).

## 7 Discussion and conclusion

In this article, I show that connectivity patterns play an important part in the intertemporal costs and damages associated with spatially distributed goods, with variable marginal costs of control. When dispersal patterns change, the optimal residual population in each patch has non-monotonous responses, as variable marginal costs of control may increase disproportionately for low stock values. On the other hand, even at low marginal control costs, large increases in inward dispersal flows may cause large increases in control costs. In the end, changes in dispersal have ambiguous effects, and patterns closer to source-sink relationships are more cost efficient.

Second, I introduce fences, that modify the patterns of spatial connectivity. If control costs are homogeneous, or dispersal is prohibitively costly to change, there is no interest in modifying dispersal, as there is no spatial arbitrage opportunity to leverage. In the case of cost heterogeneity and homogeneous biological productivity, optimal connectivity management redirects the goods towards where they are cheapest managed. However, with heterogeneous growth, or initial population, optimal connectivity management changes connectivity patterns only if

costs and growth are inversely correlated through space : in the case of large growth and costs, fencing may not be optimal, as the cost burdens can be spread through space. I then turn to the study of non-cooperative equilibria, with constant marginal costs of control. I show that in the case of exclusionary fencing, the equilibrium results in suboptimal connectivity degradation, although it fosters large levels of control in each patch, and solves the tragedy of the commons. However, in doing so, spatial arbitrage opportunities are left untapped.

The comparison between the optimal and non cooperative equilibria rests on several simplifications. First, the analysis is built on the case of interior solutions, and little care is yet devoted to the analysis of corner solutions. As eradication is favored with larger spatial independence, the analysis of the switch towards eradication in both the optimal and decentralized equilibrium lacks to fully compare the two, and is left for future work. The existing comparison nonetheless provide important insights on the management of population and connectivity, in a spatially explicit framework.

Second, the analysis rests on the assumption of constant marginal costs of control, while the original analysis of this model rests on the hypothesis of stock dependent marginal costs of control. In doing so, I avoided to consider the elasticity of control costs, which guide the evolution of optimal and decentralized residual stocks and fences, in a non monotonous fashion. While variable costs refine the analysis, the conceptual insights based on spatial arbitrage opportunity remain, in the absence of cost heterogeneity among patches.

Third, this model does not consider density dependence in dispersal patterns, which allows interior solutions to be state independent. I chose to focus on the interplay of human decisions on connectivity and population management and disentangle their relative effects rather than focusing on the evolution of population alone. I believe this structure of migration may be useful for situations where densities in each patch remain small, such that agglomeration effects of the population are too low to force migration outside of patches.

Additionally, the model developed here is not fully characterized. Overall, the effects of heterogeneity have not yet been integrated in the framework. Examples of analysis that relate the correlation of the distributions of control costs and biological productivities show that heterogeneity among patches plays an important role in the optimal management of populations and connectivity, in the case of interior solutions. This effect may be bolstered in the case of (partially corner solutions), to study how fencing promotes eradication, under what conditions does temporary fencing foster long term benefits.

I have identified four avenues of future research. First, the current two patch structure leaves global connectivity concerns difficult to study. Indeed, as this article is concerned with endogenous ecological-economic network formation, the

small scale of the analysis precludes me from deriving interesting network scale results ([Bode et al., 2008](#)), especially in the case of original invasion and optimal response of neighboring patches. . This opens the second research avenues, which involves characterizing the effects of heterogeneity on optimal network formation and population management, as well as on the decentralized equilibrium, contributing to the literature on network formation games ([Griffith, 2022](#)) in the context of renewable resources. As the effects of heterogeneity matter on small and large scale, I plan on analyzing the policy mix that can be implemented to reconcile the optimum and the non cooperative equilibrium. Intuition show that while implementing the first best policy mix, which reshuffles resources to the most cost effective patch is always best, it is not always achievable in practice. Analyzing the second best allocation is important. When a policy maker can only choose 1 instrument, i.e. either population or connectivity control, it is unclear which should be favored, and how the choice of this instrument depends on the heterogeneity of the costs, damages, growth and initial populations across the landscape. The fourth research avenue implies factoring in risk in the ecological dynamics : invasions are stochastics, and risk aversion may increase a tendency towards fencing. It is unclear how the optimal allocation of resources accounts for this effect.

## Acknowledgements

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# Appendix

## A Model timing

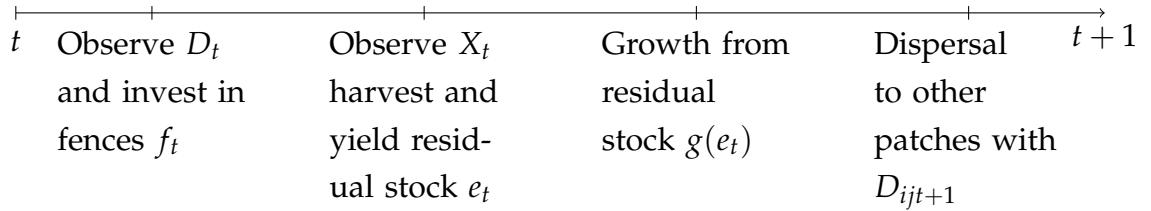


Figure 2.A: Timing of the model

## B Illustration of baseline functions for numerical illustration

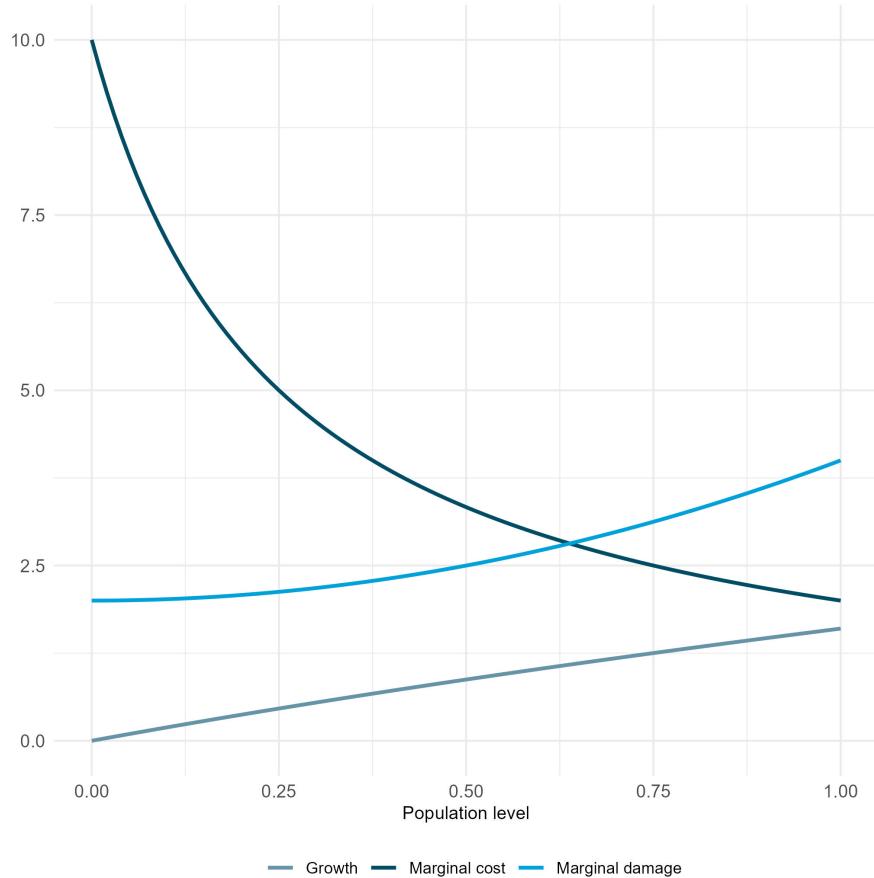


Figure 2.B: Illustration of baseline functions for numerical illustration

## C Effect of dispersal on optimal residual stock

Costello et al. (2017) define a set of first order conditions such that :

$$c_i(e_i) - k_i(e_i) = \delta g'_i(e_i)((1 - d_{ij}c_i(X_{it+1})) + d_{ji}c_j(X_{jt+1})) \quad (\text{A.1})$$

These conditions define an optimal solution as long as the second order condition is met, stemming from the convexity of the returns on control i.e. as long as :

$$SOC_i = k'_i(e_{it}) - c_i(e_{it}) + \delta g''_i(e_{it})(d_{ij}c_i(X_{it+1}) + (1 - d_{ij})c_i(X_{it+1})) \\ + \delta(g_i(e_{it}))^2(d_{ij}^2c_j(X_{jt+1}) + (1 - d_{ij})^2c_i(X_{it+1})) > 0$$

From the first order conditions, we can determine the effect of changing dispersal patterns on optimal residual stock :

$$\frac{d}{dd_{ij}} (k_i(e_{it}) - c_i(e_{it}) + \delta g'_i(e_{it})[d_{ij}c_j(X_{jt+1})(1 - d_{ij})c_i(X_{it+1})]) = 0 \\ \iff (k'_i(e_{it}) - c_i(e_{it}))\frac{\partial e_{it}}{\partial d_{ij}} \\ + \delta g''_i(e_{it})(d_{ij}c_j(X_{jt+1}) + (1 - d_{ij})c_i(X_{it+1}))\frac{\partial e_{it}}{\partial d_{ij}} \quad (A.2)$$

$$+ \delta g'_i(e_{it})(c_j(X_{jt+1}) - c_i(X_{it+1})) \quad (A.3)$$

$$+ \delta g'_i(e_{it})[(1 - d_{ij})c'_i(X_{it+1})\frac{dX_{it+1}}{dd_{ij}} + d_{ij}c'_j(X_{jt+1})\frac{dX_{jt+1}}{dd_{ij}}] = 0 \quad (A.4)$$

$$+ \delta g'_i(e_{it})[(1 - d_{ij})c'_i(X_{it+1})\frac{dX_{it+1}}{dd_{ij}} + d_{ij}c'_j(X_{jt+1})\frac{dX_{jt+1}}{dd_{ij}}] = 0 \quad (A.5)$$

The variation in residual stock is such that the current changes in marginal cost and damages caused by the change in optimal residual stock, the change in the future cost caused by (i) the growth of the population migrating along current dispersal patterns, (ii) the marginal population flow change without adjustments from the optimal stock and (iii) the marginal cost of changes in future population levels are equal. The change in future populations are :

$$\frac{dX_{it+1}}{dd_{ij}} = \frac{d}{dd_{ij}} ((1 - d_{ij})g_i(e_{it}) + d_{ji}g_j(e_{jt})) \\ = \left( -g_i(e_{it}) + (1 - d_{ij})\frac{\partial e_{it}}{\partial d_{ij}}g'_i(e_{it}) + d_{ji}\frac{\partial e_{jt}}{\partial d_{ij}}g'_j(e_{jt}) \right)$$

$$\frac{dX_{jt+1}}{dd_{ij}} = \frac{d}{dd_{ij}} ((1 - d_{ji})g_j(e_{jt}) + d_{ij}g_i(e_{it})) \\ = \left( g_j(e_{jt}) + d_{ij}\frac{\partial e_{it}}{\partial d_{ji}}g'_i(e_{it}) + (1 - d_{ji})\frac{\partial e_{jt}}{\partial d_{ji}}g'_j(e_{jt}) \right)$$

The changes in future population feature a direct effect from the change in dispersal, and an indirect effect from the marginal growth effect that follows the adaptation of optimal residual stock to changes in dispersal patterns. Reformulating equation A.5 :

$$\frac{\partial e_{it}}{\partial d_{ij}} = \frac{1}{\Omega_i} \left( \frac{\partial e_{jt}}{\partial d_{ij}} \gamma_i + \eta_i \right) \quad (\text{A.6})$$

Where :

$$\begin{aligned} \Omega_i &= k'_i(e_{it}) - c'_i(e_{it}) + \delta g''_i(e_{it}) (d_{ij}c_i(X_{it+1}) + (1 - d_{ij})c_i(X_{it+1})) \\ &\quad + \delta(g'_i(e_{it}))^2 (d_{ij}^2 c_j(X_{jt+1}) + (1 - d_{ij})^2 c_i(X_{it+1})) = SOC_i > 0 \\ \gamma_i &= -\delta g'_i(e_{it})g'_j(e_{jt}) ((1 - d_{ij})d_{ji}c'_j(X_{jt+1}) + d_{ji}(1 - d_{ij})c'_i(X_{it+1})) > 0 \\ \eta_i &= -\delta g'_i(e_{it})(c_j(X_{jt+1}) - c_i(X_{it+1}) + g_i(e_{it}) (d_{ij}c'_j(X_{jt+1}) - (1 - d_{ij})c'_i(X_{it+1}))) \end{aligned}$$

The sign of  $\eta_i$  depends on cost differential incurred by a change in the dispersal rate alone, and the marginal cost difference caused by the adaptation of the population. It is the joint effect of changing the dispersal and keeping the population unchanged, and changing the population while leaving the dispersal unchanged. Using the same method :

$$\frac{\partial e_{it}}{\partial d_{ji}} = \frac{1}{\Omega_i} \left( \frac{\partial e_{jt}}{\partial d_{ji}} \gamma_i + \Phi_i \right) \quad (\text{A.7})$$

Where :

$$\Phi_i = -\delta g'_i(e_{it})g_j(e_{jt}) ((1 - d_{ij})c'_i(X_{it+1}) - d_{ij}c'_j(X_{jt+1}))$$

$\Phi_i$  and  $\eta_i$  differ because of the absence of a direct effect as in equation A.4. These partial derivatives form a system such that :

$$\begin{cases} \frac{\partial e_{it}}{\partial d_{ij}} = \frac{1}{\Omega_i} \left( \frac{\partial e_{jt}}{\partial d_{ij}} \gamma_i + \eta_i \right) \\ \frac{\partial e_{it}}{\partial d_{ji}} = \frac{1}{\Omega_j} \left( \frac{\partial e_{it}}{\partial d_{ji}} \gamma_j + \Phi_j \right) \\ \frac{\partial e_{it}}{\partial d_{ji}} = \frac{1}{\Omega_i} \left( \frac{\partial e_{jt}}{\partial d_{ji}} \gamma_i + \Phi_i \right) \\ \frac{\partial e_{jt}}{\partial d_{ji}} = \frac{1}{\Omega_j} \left( \frac{\partial e_{it}}{\partial d_{ji}} \gamma_j + \eta_j \right) \end{cases} \quad (\text{A.8})$$

Therefore :

$$\frac{\partial e_{it}}{\partial d_{ij}} = \frac{\Phi_j \gamma_i + \eta_i \Omega_j}{\Omega_i \Omega_j - \gamma_i \gamma_j} \quad (\text{A.9})$$

$$\frac{\partial e_{it}}{\partial d_{ji}} = \frac{\gamma_i \eta_j + \Omega_j \Phi_i}{\Omega_i \Omega_j - \gamma_i \gamma_j} \quad (\text{A.10})$$

The sign of these two expressions is ambiguous, as all elements can be both positive and negative. We restrict our attention to the analysis of  $\Phi$  and  $\eta$  to un-

cover insights into the behavior of  $e_{it}$  and  $e_{jt}$ . When residual stock is large, or the discount factor is low, it is safe to assume that the denominator is positive (ultimately, the sign of the denominator depends on the relative magnitude of  $c'_i(X_{it+1})$ ,  $c'_j(X_{jt+1})$  and  $c_i(X_{it+1})$ ,  $c_j(X_{jt+1})$ ). The sign of the partial derivatives therefore depends on the numerator.

### C.1 Effect of outbound dispersal in patch $j$

Focus on  $\frac{\partial e_{it}}{\partial d_{ij}}$  and the case where it is unambiguously negative, such that  $\Phi_j < 0$  and  $\eta_i < 0$ :

$$\begin{cases} ((1 - d_{ji})c'_j(X_{jt+1}) - d_{ji}c'_i(X_{it+1}) > 0 \\ (c_j(X_{jt+1}) - c_i(X_{it+1}) + g_i(e_{it})(d_{ij}c'_j(X_{jt+1}) - (1 - d_{ij})c'_i(X_{it+1})) > 0 \\ \left| \frac{1-d_{ji}}{d_{ji}} c'_j(X_{jt+1}) \right| > |c'_i(X_{it+1})| \\ g_i(e_{it}) \left( [c_j(X_{jt+1}) + d_{ij}c'_j(X_{jt+1})] - [c_i(X_{it+1}) + (1 - d_{ij})c'_i(X_{it+1})] \right) > 0 \end{cases}$$

First, for homogeneous linear marginal costs, these are always 0: the movement of optimal dispersal depends on the sensitivity of the marginal cost. Moreover, the first term holds for small values of  $d_{ji}$  and homogeneous costs, but does not hold for larger values as  $\lim_{d_{ji} \rightarrow 1} \frac{(1-d_{ji})}{d_{ji}} = 0$ . The second term holds for specific realms of the elasticities of marginal costs (i.e.  $\epsilon_i = \frac{c'_i(X_{it+1})}{c_i(X_{it+1})}$ ). Rewriting the second condition :

$$(c_j(X_{jt+1})[1 - d_{ij}|\epsilon_j|] - c_i(X_{it+1})[1 - (1 - d_{ij})|\epsilon_i|]) > 0 \quad (\text{A.11})$$

Hence, for low values of  $d_{ij}$ , this tends to hold, while it no longer does for dispersals.

This heuristic demonstration tends to show that for moderate values of  $d_{ij}$ ,  $\frac{\partial e_{it}}{\partial d_{ij}} < 0$  and for larger values,  $\frac{\partial e_{it}}{\partial d_{ij}} > 0$ .

### C.2 Effect of inbound dispersal change in patch $i$

This second part is ongoing work.

### C.3 Numerical illustration of the effect of dispersal on optimal residual stock

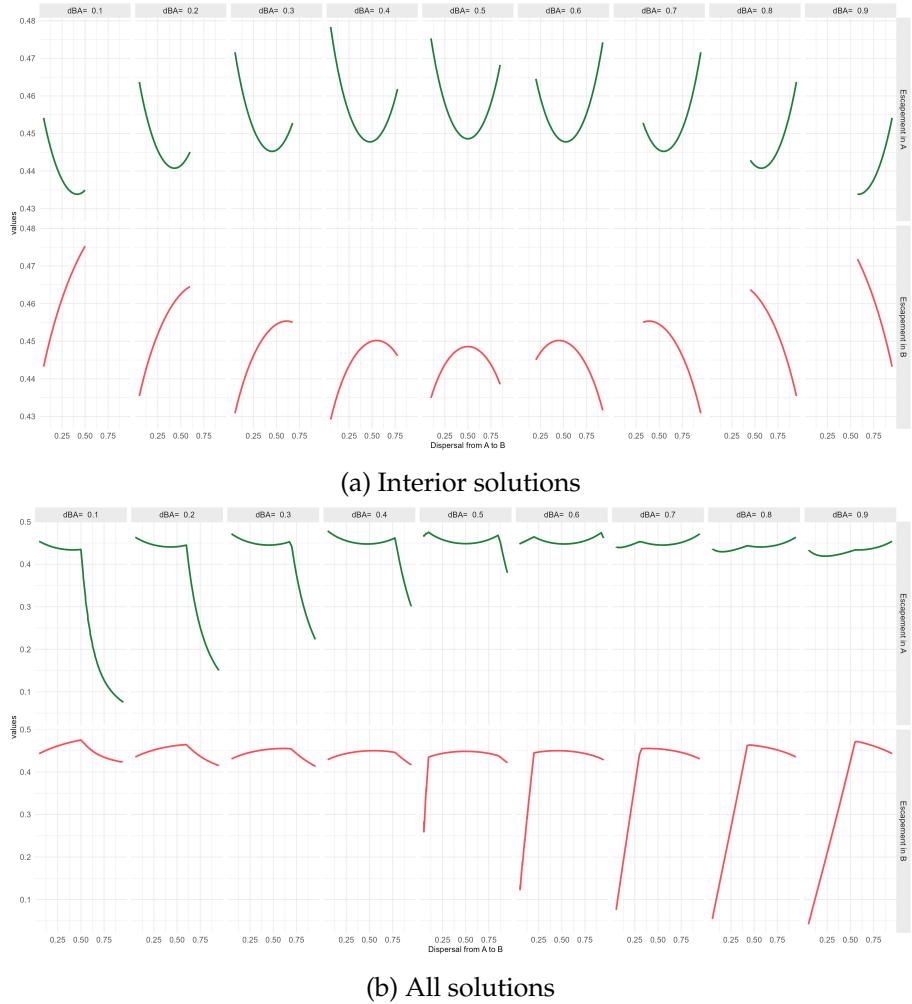


Figure 2.C: Evolution of optimal residual stock with respect to dispersal from  $A$  to  $B$  ( $d_{AB}$ )

## D Proof of changes in value following change in dispersal

In the case of interior solutions, the optimal residual stock is defined by equation 3.3 as  $e_{it}^*$ . In this case, the Bellman equation can be rewritten as :

$$V(\mathbf{X}_t, \mathbf{D}) = \sum_{i \in \{A, B\}} \left( \int_0^{e_{it}^*} k_i(s) ds + \int_{e_{it}^*}^{X_{it}} c_i(s) ds \right) + \delta V(\mathbf{X}^*, \mathbf{D})$$

Assuming we remain in the realm of interior solutions, we can use the enveloppe theorem:

$$\frac{\partial V}{\partial d_{ij}} = \sum_{i \in \{A, B\}} \frac{\partial}{\partial e_{it}} \left( \int_0^{e_{it}^*} k_i(s) ds + \int_{e_{it}^*}^{X_{it}} c_i(s) ds \right) \frac{\partial e_{it}^*}{\partial d_{ij}} + \sum_{i \in \{A, B\}} \frac{\partial V}{\partial X_{it+1}} \frac{\partial X_{it+1}}{\partial d_{ij}}$$

The first derivatives with respect to  $e_{it}$  are, by definition, equal to 0, as  $e_{it}^*$  is deter-

mined by the first-order conditions. Given that

$$\frac{\partial V}{\partial X_{it+1}} = c_i(X_{it+1})$$

and

$$\frac{\partial X_{ijt+1}}{\partial d_{ij}} = \left( -g_i(e_{it}) + (1 - d_{ij})g'_i(e_{it})\frac{\partial e_{it}}{\partial d_{ij}} + d_{ji}\frac{\partial e_{jt}}{\partial d_{ij}} \right),$$

we obtain equation 3.4.

## E Proof of socially optimal management with fences and control

Let the Bellman equation be :

$$V(\mathbf{X}_t) = \min_{\{e_{it}, f_{it}\}_{i \in \{A, B\}}} \left( \sum_{i \in \{A, B\}} \int_0^{e_{it}} k_i(s) ds + \int_{e_{it}}^{X_{it}} c_i(s) ds \right) + \delta V(\mathbf{X}_{t+1}) \quad (\text{A.12})$$

### E.1 Interior conditions for socially optimal management

Taking the first order conditions with respect to residual stock and fencing in each patch  $i$  :

$$\begin{aligned} & -c_i(e_{it}) + k_i(e_{it}) + \delta \sum_j \frac{\partial V}{\partial e_{it}}(X_{j,t+1} \leq 0) \\ \iff & -c_i(e_{it}) + k_i(e_{it}) + \delta \left( \sum_j c_j(X_{j,t+1}) \frac{\partial X_{j,t+1}}{\partial e_{it}} \right) \leq 0 \\ \iff & -c_i(e_{it}) + k_i(e_{it}) + \delta \left( \sum_j c_j(X_{j,t+1}) d_{j,t+1}(f_{jt}, f_{it}) g'_i(e_{it}) \right) \leq 0 \end{aligned}$$

Using the fact that  $\frac{\partial V}{\partial X_{it+1}} = c_i(X_{it+1})$  and  $\frac{\partial X_{j,t+1}}{\partial e_{it}} = d_{j,t+1}(f_{jt}, f_{it}) g'_i(e_{it})$ , and the fact that  $d_{i,t+1} = (1 - d_{j,t+1}(f_{jt}, f_{it}))$  setting the FOC at 0 yields equation 3.1. As  $e_{it}$  is interior, it does not depend on  $X_{it}$ .

For interior fencing levels :

$$\begin{aligned} & \kappa_i + \delta \sum_j \frac{\partial V}{\partial X_{j,t+1}} \frac{\partial X_{j,t+1}}{\partial f_{it}} \leq 0 \\ \iff & \kappa_i + \delta \sum_j \left( c_j(X_{j,t+1}) \frac{\partial X_{j,t+1}}{\partial f_{it}} \right) \leq 0 \end{aligned}$$

Using the fact that  $\frac{\partial X_{jt+1}}{\partial f_{it}} = \left( \frac{\partial d_{ijt+1}}{\partial f_{it}} g_i(e_{it}) \right)$  and  $d_{iit+1} = (1 - d_{ijt+1}(f_{jt}, f_{it}))$  yields equation 3.2. As  $f_{it}$  depends on  $e_{it}$ , which is independent of  $X_{it}$ ,  $f_{it}$  is independent of  $X_{it}$ .

These first order conditions are sufficient, if the second order conditions hold i.e  $\det(H) > 0$  where  $H$  is the Hessian matrix of the problem. I focus on this case, but further analysis is needed to ensure this holds. It is likely to hold in the case of convex control costs, but several equilibria may arise in the presence of homogeneous costs, damages and growth.

## E.2 Absence of fencing in the absence of spatial heterogeneity

Using homogeneous linear marginal costs of control :

$$\begin{aligned} k_i(e_{it}) &= c - \delta g'_i(e_{it}) [c + d_{ijt+1}(f_{it}, f_{it})(c - c)] \\ \Rightarrow c - k_i(e_{it}) &= \delta g'_i(e_{it})c \end{aligned}$$

And optimal fencing in patch  $i$  towards patch  $j$  is :

$$\begin{aligned} \kappa_i &= \delta \left( \frac{\partial d_{ij+1}}{\partial f_{it}} g_i(e_{it}) - \frac{\partial d_{j�+1}}{\partial f_{it}} g_j(e_{jt}) \right) (c - c) \\ \Rightarrow \kappa_i &= \delta \left( \frac{\partial d_{ij+1}}{\partial f_{it}} g_i(e_{it}) - \frac{\partial d_{j�+1}}{\partial f_{it}} g_j(e_{jt}) \right) \times 0 = 0 \end{aligned}$$

Hence,  $f_{it} = 0$  for  $i \in \{A, B\}$

If costs are heterogeneous (in the proof, I use linear costs, but this holds for any costs) but there is no dispersal :

$$\begin{aligned} k_i(e_{it}) &= c_i - \delta g'_i(e_{it}) [c_i + d_{ijt+1}(f_{it}, f_{it})(c_j - c_i)] \\ \Rightarrow c_i - k_i(e_{it}) &= \delta g'_i(e_{it})c_i \end{aligned}$$

And optimal fencing in patch  $i$  towards patch  $j$  is :

$$\begin{aligned} \kappa_i &= \delta \left( \frac{\partial d_{ij+1}}{\partial f_{it}} g_i(e_{it}) - \frac{\partial d_{j�+1}}{\partial f_{it}} g_j(e_{jt}) \right) (c - c) \\ \Rightarrow \kappa_i &= \delta (0 \times g_i(e_{it}) - 0 \times g_j(e_{jt})) \times 0 = 0 \end{aligned}$$

## E.3 Optimal management with heterogeneous costs and exclusionary fencing

Proposition 3.5 holds as a direct application of  $\frac{\partial d_{ijt+1}}{\partial f_{it}} = 0$ .

## E.4 Optimal management with heterogeneous costs, trap and exclusionary effects

Rewrite equation 3.2, and notice that the first-order condition only holds if for some values  $\tilde{e}_{it}$ ,  $\tilde{e}_{jt}$ ,  $\tilde{f}_{it}$ , and  $\tilde{f}_{jt}$ , equation 3.8 holds. Further, notice that if dispersal functions are identical,  $\frac{\partial d_{ABt+1}}{\partial f_{Bt}} = \frac{\partial d_{BAt+1}}{\partial f_{At}}$  and  $\frac{\partial d_{ABt+1}}{\partial f_{At}} = \frac{\partial d_{BAt+1}}{\partial f_{Bt}}$ . Finally, if  $c_A > c_B$ , the first-order conditions yield:

$$\begin{aligned}\kappa_A &= \delta \left( \frac{\partial d_{ABt+1}}{\partial f_{At}} g_A(e_{At}) - \frac{\partial d_{BAt+1}}{\partial f_{Bt}} g_B(e_{Bt})(c_A - c_B) \right) \\ \kappa_B &> \frac{\partial d_{ABt+1}}{\partial f_{Bt}} = \frac{\partial d_{BAt+1}}{\partial f_{At}} \underbrace{(c_B - c_A)}_{<0}\end{aligned}$$

Therefore, fencing can only happen in one patch.

## F Non cooperative equilibrium

### F.1 Interior MPNE

Using the Bellman equation, the first order condition for  $\bar{e}_{it}$  yield :

$$\begin{aligned}-c_i + k_i(e_{it}) + \delta \frac{\partial V_i}{\partial e_{it}} &\leq 0 \\ \iff -c_i + k_i(e_{it}) + \delta c_i g'_i(e_{it})(1 - d_{ijt+1}(f_{it}, f_{jt})) &\leq 0 \\ \Rightarrow c_i + k_i(\bar{e}_{it}) + \delta c_i g'_i(\bar{e}_{it})(1 - d_{ijt+1}(\bar{f}_{it}, \bar{f}_{jt})) &= 0\end{aligned}$$

Using the fact that  $\frac{\partial V_i}{\partial X_{it+1}} = c_i$  and  $\frac{\partial V_i}{\partial X_{jt+1}} = 0$  and  $\frac{\partial X_{it+1}}{\partial e_{it}} = (1 - d_{ijt+1}(f_{it}, f_{jt}))g'_i(e_{it})$ .

Turning to  $\bar{f}_{it}$ , recognizing that  $\frac{\partial X_{it+1}}{\partial f_{it}} = g_j(e_{jt}) \frac{\partial d_{j_{it+1}}}{\partial f_{it}} - \frac{\partial d_{i_{it+1}}}{\partial f_{it}} g_i(e_{it})$ :

$$\begin{aligned}\kappa_i + \delta \frac{\partial V_i}{\partial X_{it+1}} \frac{\partial X_{it+1}}{\partial f_{it}} &\leq 0 \\ \Rightarrow \kappa + \delta c_i \left( g_j(\bar{e}_{jt}) \frac{\partial d_{j_{it+1}}}{\partial f_{it}} - \frac{\partial d_{i_{it+1}}}{\partial f_{it}} g_i(\bar{e}_{it}) \right) &= 0\end{aligned}$$

These conditions are sufficient assuming that the second order conditions are satisfied, i.e.  $\det(H) > 0$  where  $H$  is the Hessian matrix of the problem.

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# Chapter 4

## Little downside and substantial gains result from farming of *Totoaba Macdonaldi*

This article is under review at *NPJ Ocean Sustainability* and is joint work with Julia M. Lawson (co-first author), Andrew Steinkruger, Miguel Castellanos-Rico, Garrett M. Goto, Miguel A. Cisneros-Mata, Erendira Aceves Bueno, Matthew M. Warham, Adam M. Sachs and Steven D. Gaines

Illegal wildlife trade poses a growing threat to species globally. Where bans or policy instruments have failed, conservation farming has been considered, which aims to reduce illegal poaching by “flooding the market” with farmed product. However, predicting if farming will succeed necessitates a holistic understanding of how supply and demand interact and how markets will respond. Poaching and illegal trade for totoaba (*Totoaba macdonaldi*), currently dominated by a Mexican monopolist cartel, has continued unabated despite half a century of prohibitions on international trade and domestic fishing. We investigate if farming can reduce poaching and support a healthy wild population by extending a flexible bioeconomic model of a three-stage illegal supply chain: poachers sell to traders (i.e., middlemen or cartels) who sell to end-markets. While we show under the monopolist a large stable wild population is maintained, this outcome is sensitive to cost parameters. Introducing farming decreases poaching by 29% or increases poaching by 6%, and results are robust to changes in cost parameters. Our results upend previous assertions that certain strategic responses will undermine conservation efforts and always result in population collapse. Furthermore, our quantitative framework can be adapted to evaluate conservation farming for other species and market structures.

Keywords : *Totoaba Macdonaldi*, Illegal wildlife trade, Conservation aquaculture, Monopolist Cartels, Oligopoly, bioeconomic model.

JEL codes : Q57, Q22, L12, K42

# 1 Introduction

Illegal wildlife trade is a multi-billion dollar industry that drives biodiversity loss through unsustainable harvest ('T Sas-Rolfes et al., 2019), spreads zoonotic disease (Bell et al., 2004), and threatens animal welfare (Baker et al., 2013). The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) provides a regulatory framework that aims to ensure that international trade of wild animals and plants does not threaten their survival. Yet, for many species, regulatory interventions such as trade bans and controls have failed, and illegal trade in black markets continues to flourish (Challender and MacMillan, 2014; Challender et al., 2015a). In such instances, supply-side interventions such as conservation farming can theoretically bolster conservation by “flooding the market” with farmed products, leading to reduced market prices and lower poaching incentives (Gentry et al., 2019; Phelps et al., 2014; Tensen, 2016). Supply-side interventions have occasionally succeeded at reducing poaching and recovering wild populations – e.g., vicuña and spotted cat (IUCN, 2000; Sahley et al., 2007) – but they have also failed – e.g., green python, African elephant (Lyons and Natusch, 2011; Hsiang and Sekar, 2016). Uncertainty around conservation outcomes from market-based approaches has led to continued reliance on trade bans and controls that are often ineffective at reducing poaching. Determining whether farming will succeed or fail requires a holistic understanding of a specific illegal wildlife market<sup>1</sup>, including the interplay between market conditions and ecological criteria (Challender et al., 2015b). Studies have pointed to a common set of farming pitfalls. Species with slow individual growth rates and low fecundity are often unable to grow supply quickly enough to displace illegal products. Further, if poaching is very inexpensive, it is impossible for farming to undercut prices<sup>6,8</sup> – e.g., dried seahorses are ‘free’ to poach when retained as bycatch (Lawson et al., 2017). Demand-side concerns are focused on substitutability between farmed and wild products. Consumers of wildlife for medicinal or conspicuous purposes often prefer wild products for greater perceived potency or associated social status (Dutton et al., 2011; Gratwicke et al., 2008; Fabinyi, 2012). Here, we develop a quantitative framework that comprehensively considers all these pitfalls while accounting for detailed species-specific and market information.

Another critical factor in driving the success or failure of farming is market structure: illegal markets are often characterized by imperfect competition – where an individual trader or a small number of traders (i.e., middlemen, cartels, gangs, or other criminal organizations) dominate illegal trade and exert significant control over market prices. A bioeconomic model that predicts how imperfectly competitive markets will respond to competition from farming was developed almost

two decades ago (Bulte and Damania, 2005; Damania and Bulte, 2007). Predicted strategic responses depend on how a trader chooses to compete with farming. If a trader responds by price setting (an aggressive response where the trader tries to undercut farmed prices and take market shares), then poaching pressure will increase and can lead to the collapse of the wild population. On the other hand, if traders respond by quantity adjustment (a mutually beneficial response where the trader competes on the amount of output produced, letting market prices adjust), poaching pressure is reduced and wild populations have the possibility to increase. This model has been widely used to both justify (Biggs et al., 2013; Abbott and van Kooten, 2011) and discourage (Tensen, 2016) prospective farming initiatives. The authors of the original bioeconomic model concluded that farming is a perilous coin toss (Bulte and Damania, 2005; Damania and Bulte, 2007). Here, we expand upon this model and reach a different conclusion: that farming can maintain large, stable wild population sizes that are robust to changes in cost structure under both types of competition. Furthermore, quantity adjustment yields substantial decreases in poaching and is the more likely response because prices and profits are higher than under price setting (Singh and Vives, 1984). We explore the biological and economic performance of conservation farming for totoaba swim bladder in the context of illegal poaching and trade under different market conditions (Froehlich et al., 2017). Specifically, we examine the evolution of poaching and wild totoaba biomass, as well as prices and profits for different economic actors. The lifecycle for totoaba has been successfully closed in aquaculture, and the species is currently farmed in Mexico for domestic meat production. Totoaba is endemic to Mexico's Gulf of California and is threatened by a lucrative illegal international trade for its large swim bladder (C4ADS, 2017; env, 2019, 2016). A single totoaba swim bladder can sell for up to \$80,000 USD per kilogram in Chinese end markets, where it is purchased for special occasions, gifting, and speculative investment (ElephantActionLeague, 2018; Sadovy de Mitcheson et al., 2019; Martínez and Alonso, 2021). For nearly half a century international trade for totoaba has been prohibited, and the legal totoaba commercial fishery has been closed. However, illegal fishing and trade continue and are controlled primarily by a single criminal organization (a cartel) that will likely respond strategically to farming (Damania and Bulte, 2007; Felbab Brown, 2022)

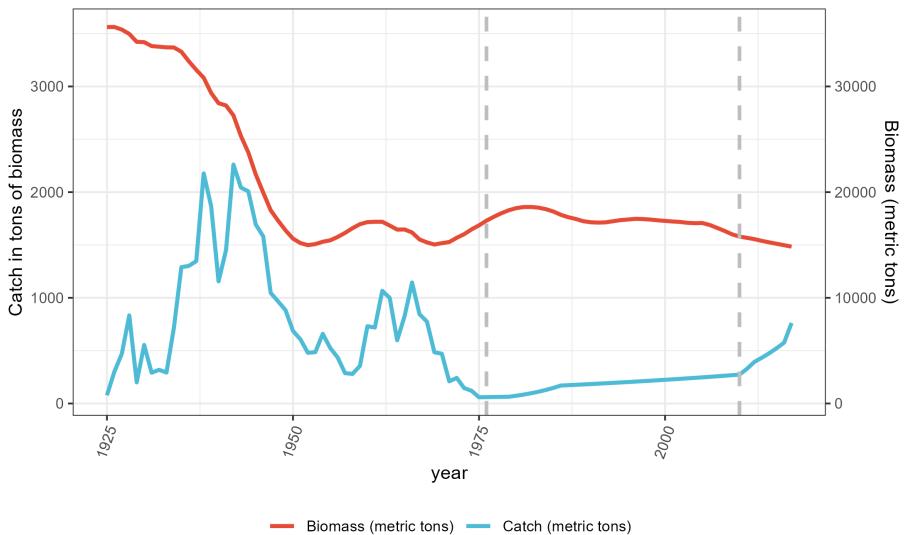


Figure 4.1: Evolution of totoaba population and catch over time

Dashed lines represent listing as CITES Appendix II species, and cartel takeover, respectively

There is an urgent need to reduce poaching for totoaba, as the vaquita (*Phocoena sinus*), a porpoise also endemic to the upper Gulf of California, is caught as bycatch in gillnets used to catch totoaba. The vaquita is on the brink of extinction as there are now fewer than fifteen individuals remaining (Rojas-Bracho et al., 2022). Furthermore, illegal trade has had negative social welfare consequences, as cartels are increasingly extorting Mexican fishing communities (Felbab Brown, 2022). Despite Mexico's attempts to stop totoaba poaching through various enforcement mechanisms, the country recently received wildlife trade sanctions for taking inadequate action (Rojas-Bracho and Reeves, 2013; CITES, 2023). Conservation farming presents a legal alternative to reduce illegal fishing by manipulating market structure.

We assemble and leverage a unique wealth of information on the totoaba stock, poaching sector, and farming sector to estimate the effects of market structure on poaching harvest and stock biomass. We focus on the market structure that best characterizes the totoaba trade – a vertical monopoly where a single monopolist trader controls the entire supply chain – and evaluate how this trader will respond strategically to competition from farming. We also show how to identify an effective policy space, where all supply, demand, and market structure parameters align to ensure that conservation farming will reduce poaching. Our results challenge long-standing model conclusions (Bulte and Damania, 2005; Damania and Bulte, 2007), thereby disrupting widely-held beliefs about the impacts of conservation farming. In particular, previous studies cautioned that when a trader responds to farming through price setting, the wild population always declines dramatically. In contrast, we find that for totoaba, price setting can maintain a stable and large population given that as the population size decreases, fishing

costs increase. To ensure low retail prices, traders must limit the price they pay to poachers and maintain a viable wild population.

## 2 Methods

We examine the effect of market structure and competition on poaching a population of wild animals using the logistic growth function (Figure 4.2). The poaching harvest function intersects with population growth producing stable and unstable equilibria. If poaching pressure is high relative to population growth (i.e, when demand is large, or poaching costs are low), a single stable equilibrium point is observed with a low wild abundance (an overharvested population). In the opposite scenario, where poaching pressure is low relative to population growth (i.e, when demand is small, or poaching costs are prohibitive), a single stable equilibrium point is observed with a high wild abundance (a healthy population). Between these extremes, two or three potential equilibria can emerge, with uncertain results that depend on the initial size of the population: a large initial population will result in a high abundance equilibrium point, and a small initial population will result in a low abundance equilibrium point.

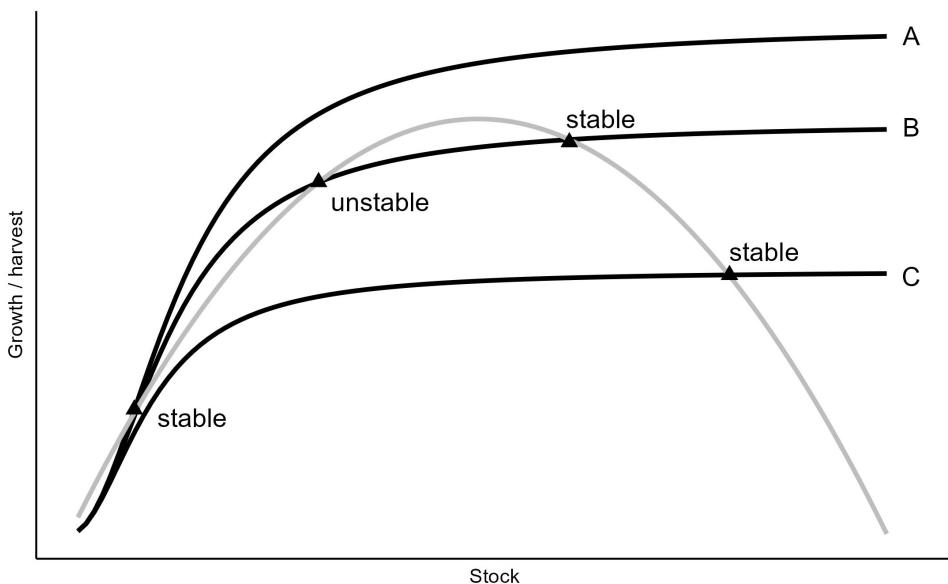


Figure 4.2: Schematic of equilibrium points under different poaching harvest functions

Logistic growth function (light gray) showing equilibria points resulting from three hypothetical poaching harvest functions (black). (A) a single low stable equilibrium point; (B) uncertain outcome, three interior equilibria two of which are stable and one unstable and separating. The long run equilibrium point will depend on the initial size of the population. A large initial population will result in a high abundance equilibrium point, and a small initial population will result in a low abundance equilibrium point; (C) a single high stable equilibrium point.

To assess expectations for totoaba, we first calculate equilibrium points for the stock in the absence of conservation farming under vertical monopolistic conditions (hereafter referred to as monopolistic conditions for ease) (Figure 4.3). A

single trader exists in a single location where he is the sole buyer, typical of endemic species such as totoaba (Wyatt et al., 2020; Martinez-Alvarado and Martinez, 2018). The trader sells poached harvest on an end market where prices and quantities can be manipulated.

Next, we add conservation farming to the monopolistic market structure, creating a duopolistic market (Figure 4.3). We calculate equilibrium points for the totoaba stock if a monopolistic trader responds to conservation farming either in a way that is (a) mutually beneficial by quantity adjustment or (b) aggressive by price setting. From a policy assessment perspective, any scenario where poached harvest produces a single high stable equilibrium point, and the monopolist cartel loses income, presents clear conservation and social welfare benefits.

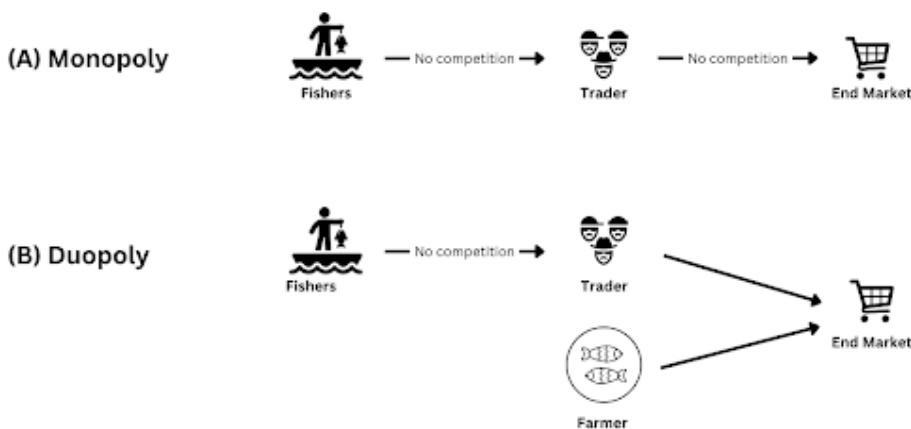


Figure 4.3: Schematic of monopoly and duopoly market structures

(A) monopolistic conditions, where fishers sell to a single trader where they are the sole buyer. This single trader sells poached harvest on an end market where they can manipulate prices and quantities. (B) Next, we add duopoly with farming: A monopolistic trader responds to conservation farming either in a way that is mutually beneficial by quantity adjustment or aggressive by price setting.

Here we briefly discuss our methods with an emphasis on the empirical application. Information on our theoretical conclusions from the bioeconomic model we revisited, lemmas and proofs can be found in the Appendix, section B. Table 4.J summarizes all the functions of the model.

## 1 The Poaching Model

The growth of the fish stock follows a logistic curve and the stock is poached following a Gordon-Schaefer production model. Totoaba population growth parameters were obtained from the 2017 stock assessment, where the carrying capacity ( $K$ ) was 20,226 mt, and the stock biomass in 2017 was 14,844 mt (Cisneros-Mata, 2020). The intrinsic rate of population increase ( $r$ ) was predicted using the *FishLife* package in R, which estimates growth parameters using totoaba-specific life

history data from *FishBase* (Thorson et al., 2017). The growth equation is :

$$g(x) = rx \left(1 - \frac{x}{K}\right) \quad (4.1)$$

using a predicted  $r$  of 0.20. We do not consider potential effects of hyperstability of the stock resulting from poaching on seasonal spawning aggregations (Erisman et al., 2011) or age structure.

Poachers optimally determine their effort to maximize their profit, with constant catchability  $\sigma$ , and stock biomass,  $x$ , obtained from the 2017 stock assessment<sup>46</sup>, and a linear quadratic cost of effort function,  $E$ . The poaching equation is  $q = \sigma x E$  where  $\sigma = 0.00002$ .

Poachers are faced with a linear quadratic cost function  $C(E) = W_1 E + W_2 E^2$ . We calculated two poaching cost parameters  $W_1$  (the linear coefficient of the cost function) and  $W_2$  (the quadratic coefficient of the cost function) by (a) estimating total and average annual operating costs of the fishing fleet using semi-structured interviews conducted by the authors of this study; and (b) calibrating a linear quadratic cost function that matches historical data and predicts future cost evolution.

We conducted semi-structured interviews in the upper Gulf of California with two fishing cooperative leaders and four fishers in July and August 2018. These interviews informed annual poaching costs: food and fuel, labor, gear replacement, and bribes paid to fisheries officials. The fishery operates over six months with a variable number of active vessels, monthly fishing days, and sets per day (Cisneros-Mata, 2020). Poaching costs also include annual fleet-wide costs related to gear confiscations, vessel replacement, and fines, adapted and extrapolated from a summary of law enforcement actions provided by Mexico (noa, 2018). The cost per fishing trip was estimated to be \$5,051.26 during the low season (January and June), \$8,385.34 during the mid-season (February and May), and \$14,386.7 during the high season (March and April) (supplementary table 4.F). In our analysis we reconstructed a linear quadratic cost function with cumulative effort. We considered effort in each season cumulative with effort in less intense seasons. We used a low-season average cost for effort levels between 0 and low-season effort; for effort levels between low-season effort and cumulated low and mid-season efforts, we used a mid-season average cost.

We estimated the corresponding poaching cost parameters to match the observed average cost and modeled marginal costs at historical levels (resulting in cost parameters  $W_1 = 12,200$  &  $W_2 = 0.57$ ). Our low sample size precludes a robust statistical estimation of these cost parameters, e.g., of the historical cost function and of the evolution of costs if the fishery were to increase. To account for this uncertainty, we run a sensitivity analysis on two dimensions of costs.

First, we use different estimates for the average cost and reconstructed total costs, ranging from  $-10\%$  to  $+30\%$  of our high season average cost estimates. Second, we test weights for the linear and quadratic costs, ranging from a purely linear cost ( $W_1 = 14,386,7$ ,  $W_2 = 0$ ) to a purely quadratic cost ( $W_1 = 0$ ;  $W_2 = 3,74$ ).

The resulting poaching profit function is calculated as follows:

$$\Pi = p\sigma xE - W_1E - W_2E^2 \quad (4.2)$$

Traders operate on the end market, taking prices as given (competitive scenario) or determining prices (monopolistic scenario) to maximize profits. Traders face a linear demand function. We estimate a linear demand function by regressing price data on estimated catch from 2014 to 2017<sup>46</sup>, yielding the equation  $p(q) = \alpha - \beta q$  where the intercept,  $\alpha$ , is \$1,625,837 USD and the slope coefficient,  $\beta$ , is \$1,563.75 USD (see supplementary table 4.G). Price data were obtained from available literature that provided estimated weight and value of totoaba maw seizures<sup>24,26,50,51</sup>. In addition to the literature review, valuable insights were obtained through personal communication with Wild Aid Investigators (pers. comm. Anonymous Wild Aid Investigators, 2018) as well as with local fishers and cooperative leaders in the upper Gulf of California, as previously described. The information shared by investigators and stakeholders was aggregated with the existing data from the literature. To ensure consistency and comparability, we standardized the weight measurements to grams and the currency values to US dollars. We assume that annual catch reaches the market during the same year, i.e, there is no stockpiling. As data are notoriously difficult to acquire for illegal trade, we pool observations and estimate a stationary demand function (supplementary table 4.G).

Traders buy totoaba from poachers at **price**  $s$  (USD/metric ton). The price paid to poachers balances demand from traders and supply to poachers. It decreases as the population increases, as fishing becomes less demanding. Traders also pay a unit transaction cost  $c$  (USD/metric ton), which we conservatively estimated to be zero. At a minimum this unit transaction cost includes transport (land and air travel), and payment to two or three ‘runners’ who carry up to ten swim bladders each (pers. comm. Anonymous Wild Aid Investigators, 2018). We know through anecdotal evidence that unit transaction costs  $c$  are likely large (ElephantActionLeague, 2018). However, due to scarce evidence, we used a value of  $c = 0$  thus adopting a conservative strategy.

## 2 The Farming Model

We use a linear profit model for aquaculture and estimate a unit farming production cost parameter  $v$  (USD/metric ton) using annual operational costs (la-

bor, feed, vessel fuel, facility and administrative fees), as well as annual maintenance of pens (including cleaning) and vessels, using information provided by existing aquaculture facilities (supplementary table 4.H). Population growth rates differ in the wild and in captivity. Using captive growth rates obtained from personal communication with totoaba aquaculture producers, we consider harvestable size to be between 4.5 and 5 years old (an adult weight of 21.43 – 27.2 kg), associated with a swim bladder size between 417 – 529 g (supplementary figure 4.E). A minimum farmed harvestable size of 4.5 years closely corresponds to the mean swim bladder size (500 g) and estimated adult totoaba size (25.7 kg), as reported in surveys of individuals harvested in the wild ([Cisneros-Mata, 2020](#)). We considered this to be the size at which farmed totoaba would be competitive with the average wild-caught totoaba. We assume that aquaculture operates on a homogenous rotation ([Faustmann, 1849](#); [Mitra and Wan, 1986](#)). The implications of this assumption are discussed in the appendix A.3. We compute the farming cost per metric ton as the capitalized sum of annual costs over 4.5 years at a 10% interest rate.

### 3 Demand

We use a linear demand function in the case of the vertical monopoly, estimated using price and catch data from 2014 to 2017 (see table 4.G), such that  $p^w = \alpha^w - \beta^w q^w$ . Upon the introduction of aquaculture, following [Singh and Vives \(1984\)](#) and [Damania and Bulte \(2007\)](#), we include a substitutability parameter  $\gamma$ , which measures the imperfect substitutability between farmed and wild products in the linear demand functions. When farmed products are introduced, the linear demand function is modified such that  $p^i(q^i, q^k) = \alpha_i + \beta_i q^i + \gamma q^k$  where  $q^i$  and  $q^f$  indicate the supply from the wild (*w*) and the farmed supply (*f*). This demand system emerges from a linear quadratic utility function in Supplementary Text (section 1.3.2). When demand intercept  $\alpha_i$ s are equal, and own price effect  $\beta_i = \beta_j = \gamma$  are equal, products are perfect substitutes. When demand intercepts are equal, but own price effects differ ( $\beta_i \neq \beta_j$ ), then  $\frac{\gamma^2}{\beta_i \beta_j}$  denotes the degree of product substitutability. At present, there has been no stated preference investigation for wild and farmed totoaba swim bladders in Chinese end-markets, although we know that the end-market economic value for fish maw is determined by taxon, size, and thickness of swim bladder. Investigative work in Mexico reports that it is challenging to distinguish between wild and farmed specimens ([ElephantActionLeague, 2018](#)). Therefore, we assume high substitutability (75% product substitutability) and check for smaller substitutability values in our sensitivity analysis (Figure 4.7) (see supplementary table 4.I) for a list of parameters).

### 3 Results

#### 1 Totoaba stock under monopoly is sensitive to cost structure

We revisit and expand upon a bioeconomic model developed nearly two decades ago which differentiates between poachers and traders and develops a three-stage game ([Bulte and Damania, 2005](#); [Damania and Bulte, 2007](#)). The totoaba is an endemic species that is illegally traded by a single trader, a monopolist, who dominates the market. This is the market structure that best characterizes the present consolidated totoaba trade ([Felbab Brown, 2022](#)). In this setting, a single monopolist trader restricts the supply of wildlife products to consumers, leading to increased prices and profits for the monopolist.

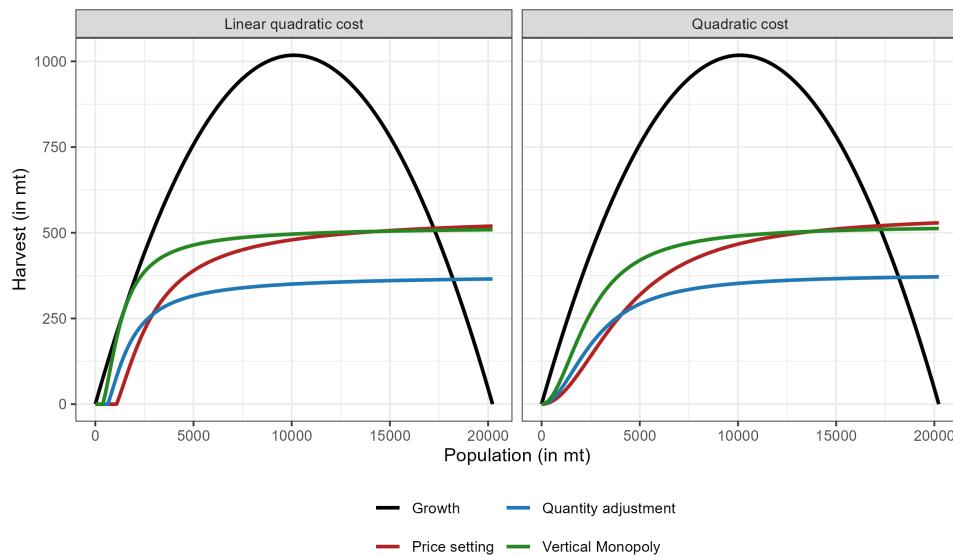


Figure 4.4: Equilibrium points for wild totoaba stock under different market structures with (left) a linear quadratic cost structure, and (right) a quadratic cost structure.

Logistic growth function (black) for *Totoaba macdonaldi* wild stock biomass with intersecting colored lines representing different market structures and competitive responses. Harvest under the status quo vertical monopoly is represented by the green curve. When conservation farming is added to the monopoly scenario the trader can respond either in a mutually beneficial way by adjusting the quantity supplied given a market price (quantity adjustment, in blue). Alternatively, the trader can respond aggressively and try to set a price that undercuts the price of farmed products, resulting in increased poaching (price setting, in red)

We initially calculate equilibrium points for totoaba assuming a quadratic cost structure, consistent with the original model, before calculating equilibrium points under a linear quadratic cost structure (Figure 4.4). Under the quadratic cost structure used in the original bioeconomic model, the totoaba wild stock biomass remains at a high steady-state equilibrium of 17,259 mt. However, we expand upon the quadratic cost structure, introducing a linear quadratic cost structure to account for energy costs associated with fishing. A linear quadratic cost structure more accurately represents new poachers being recruited to the

fishery as fishing opportunities increase (Péreau et al., 2012; Clark, 2007).

We find that under monopoly the linear quadratic cost structure is sensitive to cost parameter specifications, where relatively small changes in cost parameters can cause multiple steady states to emerge (Figure 4.5). If an increase in poaching comes at a small cost increase compared to historical average costs, the aggregate cost is close to linear (e.g.  $W_2 = 0.47$ ) and below, compared to baseline  $W_2 = 0.57$ ). In this case, a low steady-state equilibrium of 1,106 mt, an unstable intermediate equilibrium arises at 1,842 mt and a high stable steady-state equilibrium of 17,277 mt in the vertical monopoly. Our model uses the best available information on the totoaba fishery, but uncertainty surrounding the projected evolution of fishery-wide poaching costs warrants a cautious assessment of monopoly performances: while it could maintain a healthy population, it can also lead to stock collapse.

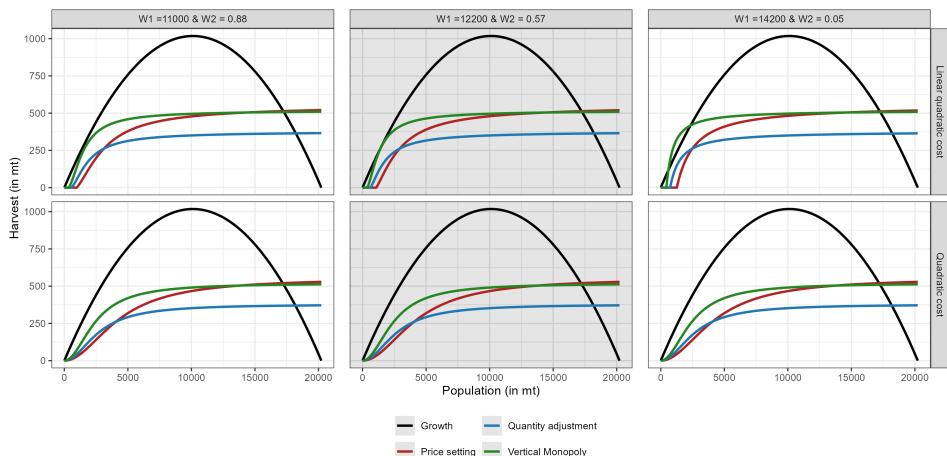


Figure 4.5: Sensitivity of equilibrium points to cost structure for wild totoaba stock

Logistic growth function (black) for *Totoaba macdonaldi* wild stock biomass with intersecting colored lines representing different market structures and competitive responses. Harvest under the status quo vertical monopoly is represented by the green curve. When conservation farming is added to the monopoly scenario the trader can respond either in a mutually beneficial way by adjusting the quantity supplied given a market price (quantity adjustment, in blue). Alternatively, the trader can respond aggressively and try to set a price that undercuts the price of farmed products, resulting in increased poaching (price setting, in red). Cost parameters  $W_1$  and  $W_2$  correspond to the linear quadratic cost structure. In the top panel, equilibria are displayed for the linear quadratic cost, on the bottom, for a quadratic cost. On the left panel, the quadratic component is large, and vertical monopoly maintains a healthy stock. Center panel highlights the baseline scenario. In the right panel, the cost structure is close to linear. In this case, the vertical monopoly may lead to drastic stock decline.

## 2 Farming produces conservation benefits

While our results show that totoaba stock may remain healthy under the current monopolistic market conditions, these results are sensitive to changes in poaching costs (Figure 4.5). Therefore, we ask if conservation farming can improve upon

the status quo by producing a robust single high stable equilibrium point and reduced cartel profits.

We add conservation farming to the monopolist model and now have two ‘firms’ – a trader and a farmer – competing on a duopolistic market. When farming supplies legal product to end-market consumers, the demand for illegal product will fall, assuming that wild and farmed products are substitutable (an assumption we explore later). The monopolist trader can respond to competition in two ways: a mutually beneficial way by adjusting the quantity supplied given a market price (quantity adjustment), or alternatively, an aggressive way that tries to select a price that undercuts the price of farmed products (price setting). In both scenarios, the trader and farmer choose a quantity supplied simultaneously, without knowing how the other will respond.

Illegal markets are almost always characterized as competing through quantity adjustment (Poret, 2009; Flores, 2016). Under the assumption that products are substitutable, it is more profitable – and therefore more likely – for both firms to compete through quantity adjustment (Singh and Vives, 1984). When goods are substitutes, if both firms restrict the quantities supplied, they both enjoy higher prices. If they flood the market, prices and profits collapse. In the case of totoaba, we find that if traders respond through quantity adjustment under the linear quadratic cost structure, then the wild stock biomass increases by 5.45% (compared to a monopoly) to a steady state equilibrium of 18,220 mt, or to 90% of carrying capacity (Table 4.6). This represents a reduction in poaching harvest of 28.27% and \$195.16 million USD of annual lost profit to the trader.

Even if traders respond aggressively through price setting, considered a less likely response (Singh and Vives, 1984) a single high equilibrium emerges (Figure 4.4). Price setting is considered a much less likely response to competition because the trader would face steep profit losses. Under the high steady-state equilibrium with the linear quadratic cost structure, wild stock biomass decreases by 0.24% relative to monopoly, to a steady-state equilibrium of 17,235 mt, or to 85% of carrying capacity (Table 4.6). Although the high steady-state reflects a relatively small increase in poaching harvest by 5.85%, it would result in \$313.84 million USD of annual lost profit to the cartel, making this strategy unlikely.

Our current specifications for totoaba show that price setting leads to a slight increase in poaching pressure, however, we argue that price setting does not universally lead to increased poaching pressure, challenging a key conclusion from the original bioeconomic model (Bulte and Damania, 2005; Damania and Bulte, 2007). Farming puts an upper bound on the price traders can pay to poachers in order to remain competitive. When the cost of farming becomes lower than the combined cost of poaching and trading, price-setting competition does not inevitably result in the overexploitation of the wild stock. This is because

Scenario	Poached harvest (in mt)	Farmed harvest (in mt)	Steady state population (in mt)	Illegal profit (in million USD)	Farming profit (in million USD)	Fishing profit (in million USD)	Aggregate profit (in million USD)	Illegal profit change (in million USD)	Variation in ss. pop.	Poaching change (%)
Vertical Monopoly	507.04	0.00	17277.0	402.02	0.00	1.22	403.24	0.00	0%	0%
Quantity adjustment	363.71	333.60	18220.5	206.87	174.03	0.57	381.46	-195.16	5.46%	-28.27%
Price setting	536.70	430.05	17235.0	88.18	58.74	3.57	150.49	-313.84	-0.24%	5.85%

Bioeconomic performance

Figure 4.6: Economic and ecological performance of different market regimes

when farming costs are low, traders have an incentive to maintain large stocks by poaching less to remain competitive with farmers. This limits the price paid to poachers. On the other hand, when farming costs are large, traders have an incentive to poach more, paying a larger price to poachers while remaining competitive with the farming sector. In the case of totoaba, species specific traits and market characteristics result in a slight increase in poaching in the price setting scenario. However, if the carrying capacity were smaller, or demand lower, the price-setting equilibrium would result in conservation benefits.

While we focus on the effect of conservation farming on a monopolistic market structure, given that this scenario best represents the totoaba fishery today, the effect of conservation farming on market structures can be explored in different contexts. We model alternative market structures, including scenarios with multiple competing traders or multiple competing farmers, and find that if the number of farmers exceeds the number of traders, poaching levels will decline (supplementary figure 4.A). Additionally, if farming is taken over by monopolists, we find that poaching is reduced and the wild population increases (supplementary figure 4.B).

### 3 An effective policy space for farming.

Our analysis provides a quantitative framework that can identify an effective policy space where all supply, demand, and market structure parameters align to ensure that conservation farming will reduce poaching, improving greatly on the original bioeconomic model and the limitations of binary qualitative approaches (Phelps et al., 2014; Tensen, 2016; Bulte and Damania, 2005; Damania and Bulte, 2007; Challender et al., 2019). This bioeconomic model allows researchers to quantify: (a) how much cheaper farming must be relative to poaching to be competitive; (b) how much of a demand increase can be absorbed by farming; and (c) how substitutable must wildlife products be for farmed products to displace wild products. Critically, we also explore how the interaction between these fac-

tors may affect outcomes. We explore how sensitive the results are for totoaba, offering general and totoaba-specific policy solutions to help ensure that conservation farming remains in the effective policy space.

We find that the cost of conservation farming for totoaba can be high and still competitive with poaching, but this is contingent on the cost for traders also being high (supplementary figure 4.D). Traders inherently rely on poachers to obtain totoaba, and if farming is expensive this forces traders to pay poachers higher prices. If traders compete with poachers under the more likely quantity adjustment response, the population remains healthy, even increasing by nearly 6% from the monopoly steady state. However, if traders compete with farmers by price setting, the low prices paid to poachers can incentivize poachers to increase fishing pressure in order to maintain payouts. This can lead to a decrease in the wild population biomass modestly by 0.24% from the monopoly steady state. Policymakers can support farming success by subsidizing farming to keep the cost low while maintaining enforcement to keep the cost of poaching high (for totoaba this includes marine patrols, fisheries closures, and gillnet bans). To mitigate the possibility of stock decline under the less-likely price-setting response, we identify that maintaining conservation farming below \$77,339 USD per mt of totoaba (amounting to a 14% subsidy on unit production cost) will prevent any increase in poaching pressure under either competitive response, assuming no effect of law enforcement in our baseline model.

Our results confirm that high substitutability is critical to conservation farming success and leads to larger conservation benefits in the quantity-setting equilibrium, under the assumption that demand remains stable (Figure 4.7). Fish swim bladders have a wide variety of uses and values, and it is possible that farmed totoaba swim bladders may enter into these different product streams ([Sadovy de Mitcheson et al., 2019](#)). In the case of no substitutability, two separate, non-competitive markets emerge. In this scenario the status quo is maintained, both firms set high prices, and traders continue to operate as a monopoly because farmed product does not compete with wild product. At the other extreme, in the case of perfect substitutability, consumers prefer the cheaper option without any preference of source. This increases the intensity of potential price-setting competition between firms and further depletes the stock in this case. To comply with CITES captive breeding guidelines totoaba must be identified as farmed ([CITES, 2019](#)), and distinguishing between products to meet regulatory obligations can artificially lower substitutability. Outcomes vary under intermediate states of substitutability. For low to medium substitutability (i.e., 10 – 50%) traders and farmers are still likely to limit quantity: undercutting a competitor would yield significant profit losses. For high substitutability (i.e., 90%) there is an incentive to compete for market control either by price setting or quantity adjustment, which

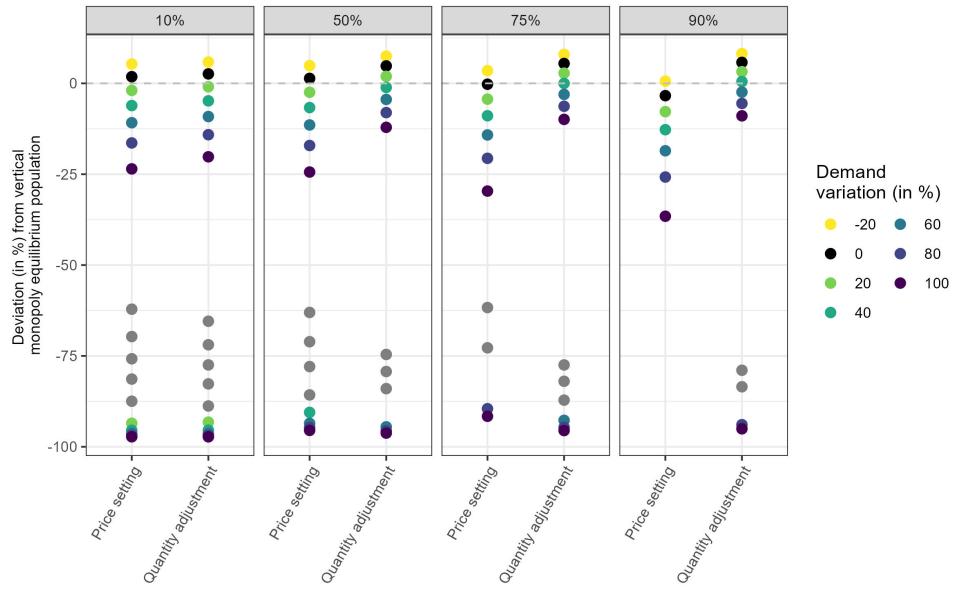


Figure 4.7: Interaction between substitutability and demand under duopolistic competition

Each panel represents a different substitutability between farmed and wild product: large (90% substitutability), baseline (75%), medium (50% substitutability), and low (10% substitutability). Our baseline results are in the 75% substitutability case, with zero demand variation (black dots). When conservation farming is added to the monopoly scenario the trader can respond aggressively and try to set a price that undercuts the price of farmed products (price setting), alternatively the trader can respond in a mutually beneficial way by adjusting the quantity supplied given a market price (quantity adjustment). We simulate a change in end-market demand ranging from a reduction in demand by 20% to an increase in demand up to 100%, in increments of 20%. One, two, or three potential equilibria can emerge. Where three equilibria points emerge, we color only the high and low stable equilibria (unstable equilibria are indicated in gray). The dotted horizontal lines indicate the status quo monopoly equilibrium population (in the absence of conservation farming). Points closer to 0 represent a high stable equilibrium point, whereas points closer to  $-100$  represent a population collapse stable equilibrium point.

reflects our main results.

The value of totoaba swim bladder is tied to rarity, and while demand evolution is an open empirical question, we test the sensitivity of our results to simultaneous changes in demand and substitutability (Figure 4.7). Totoaba swim bladder purchases are ‘conspicuous consumption,’ luxury products commonly purchased for social status and speculative investing by wealthy consumers ([Sadovy de Mitcheson et al., 2019](#); [Veblen, 2023](#)). A decrease in swim bladder price resulting from conservation farming may actually undermine the desirability of totoaba swim bladders in Chinese end markets, given that the high monetary value is linked to high social status ([Jinkins, 2016](#)). However, some increase in demand may be expected if a legal product becomes available, as law-abiding consumers will be more likely to purchase wildlife products when those products are traded and purchased legally ([Phelps et al., 2014](#)). Under our high substitutability as-

sumption (75%), competition through quantity adjustment can withstand a 40% increase in demand, whereas competition through price setting is not robust to demand increases. For price setting, a demand increase of 40% would cause the equilibrium population to decrease by 10% from the monopoly status quo, increasing poaching by 216 mt.

There is a much higher threat to the wild population if demand increases under low to medium substitutability (i.e. 10 – 50%), given that this additional demand cannot be fully met by farmed product (Figure 4.7). In the best-case and most likely scenario, medium substitutability (50%) can meet a 20% increase in demand if competition occurs through quantity adjustment, although uncertain outcomes (e.g. high and low steady states) start to emerge if demand increases by 60% or more. In the worst-case scenario, if competition occurs through price setting and products have medium substitutability (50%), any increase in demand reduces the wild population from the status quo. While increases in demand of 20 – 40% still produce a single high equilibrium point, the population size is lower than under monopoly. Furthermore, if demand increases beyond 80%, uncertain outcomes emerge, with the wild population either stabilizing at a high equilibrium point (14,322 mt in the price setting scenario; 15,886 mt in the quantity adjustment scenario) or being pushed to a low equilibrium point (ranging from 763 mt in the quantity adjustment scenario; 909 mt in the price setting scenario). We recommend that stated preference investigations on wild versus farmed product should be undertaken in Chinese end-markets and that these investigations include questions focused on perceived social status benefit and legality ([Hinsley and 't Sas-Rolfes, 2020](#)).

## 4 Conclusion

Our results show that conservation farming presents a potentially high reward intervention. If traders respond to competition from farming by quantity adjustment, the wild totoaba stock is predicted to increase by 5.45% relative to the status quo monopoly, to a high stable biomass of 18,220 mt (90% of carrying capacity). In addition to improving the totoaba wild stock, this quantity adjustment response will decrease poaching by 28.27% relative to the status quo. If traders respond by price setting, the wild stock biomass decreases by less than 1% to a high stable biomass of 17,235 mt (85% of carrying capacity). Economic theory concludes that quantity adjustment is the more likely outcome because restricting quantities allows both farmers and traders to collect higher profits ([Singh and Vives, 1984](#)). Conservation farming presents a more robust outcome to the status quo monopoly market structure (where a single trader dominates the market), as the wild totoaba reaches either a low or high stable equilibrium biomass

depending on the poaching cost structure. We find that if products have high substitutability they are more likely to maintain a high stable equilibrium. Further, under a quantity adjustment response, highly substitutable products can better maintain this high stable equilibrium for demand increases up to 40%. Our results are sensitive to changes in substitutability and increases in demand, therefore we encourage a thorough understanding of end-market demand before implementing conservation farming for totoaba.

We revive an existing bioeconomic model and reach different and optimistic conclusions about the potential for conservation farming to reduce poaching and maintain a healthy wild population. We provide a novel framework to objectively assess the potential effects of farming by grounding our analysis in detailed species ecology and market data. Furthermore, our approach provides a rigorous alternative to existing qualitative frameworks that are unable to analyze the interaction between multiple variables. While our analysis focuses on totoaba, the bioeconomic model is flexible and can be applied more broadly to other species and contexts to examine the effect of conservation farming on a wild population.

## Acknowledgements

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## Contributions and data availability

J.M.L and S.J contributed to this work equally. J.M.L., S.J., M.C-R., G.M.G., M.A.C-M., E.A-B, and S.D.G. contributed to writing the manuscript. J.M.L., S.J., A.S., and S.D.G. contributed to study conception and design. All authors contributed to data acquisition and analysis. All authors approve of the submitted manuscript. The data that support the findings of this study are available [here](#). The code used for this study is publicly available on [Github](#) and [archived here](#).

# Appendix

## A A theoretical model of poachers, traders, and farmers

Our framework follows [Damania and Bulte \(2007\)](#), with a poaching cost structure adapted to fisheries. The model develops a three-stage dynamic, game theoretic, bioeconomic model. The value chain for poached animal products comprises poachers, middlemen traders, and end markets. As a small number of actors characterizes many wildlife markets, the model features a vertical monopoly and looks at the consequences on wildlife population stocks of the introduction of a farmed substitute. In this setting, farmers compete on end markets with traders in quantity and price. In the original model, price competition unambiguously results in larger harvests than in the vertical monopoly case. Therefore, while quantity competition reduces poaching, the threat of a population collapse in the price-setting case should warrant a cautious approach to conservation farming. We argue that this conclusion is erroneous, as the intricacies of imperfect substitutability and market dynamics have not been properly accounted for in the original model. As a matter of fact, standard economic intuition regarding price-setting competition in the homogeneous goods case does not directly apply here, as fishing costs rise as the stock decreases, limiting the ability of the trader to flood the market. We show that scenarios exist where any type of competition unambiguously leads to positive conservation outcomes, i.e., reduced poaching and larger steady-state stocks. We amend the original results and use this model for simulation.

First, poachers illegally harvest wildlife resources. Second, they sell their catch to a monopsonistic buyer. Third, the buyer sells catches on a monopolistic market, which is not accessible to poachers. We label this value chain 'vertical monopoly' as a reference case. We then look at the impact of introducing a competitor on the end market, the farming sector.

### A.1 Entry in the fishery and poaching supply

We denote the fishing effort by  $E$ , which is measured in the number of vessel trips. Entry in the poaching sector,  $\dot{E}$ , is a function of payoff and an adjustment parameter. Harvest,  $q$ , follows the Gordon-Schaefer dynamic biomass model  $q = \sigma x E$ , with  $\sigma$  the (stock-independent) catchability coefficient, and  $E$ , effort. The payoff is determined by the price paid to the poachers  $s$  minus the cost of effort. We adopt a disaggregated view of the fishery, and consider increasing marginal costs of effort, as individuals have to be attracted from other activities with increasing opportunity costs. To account for energy costs, we derive a modified version of this model using a linear-quadratic cost function (see [37, 53]). Entry happens as

long as the profit of the marginal poacher is positive :

$$\dot{E} = \eta \frac{d\Pi}{dE} = \eta \frac{d}{dE} [sq - W_1 * E - W_2 E^2] \quad (\text{A.1})$$

The resource stock biomass  $x$  follows a logistic growth curve and is harvested. Overall, the dynamics are:

$$\dot{x} = g(x) - q = rx \left(1 - \frac{x}{K}\right) - \sigma x E \quad (\text{A.2})$$

Where  $r$  is the intrinsic population growth rate, and  $K$  is the carrying capacity.

Fishermen enter the fishery as long as the marginal profit from selling to traders along the vertical value chain is positive. As the resource is in open access from the fishermen poachers maximize their instantaneous profit with respect to effort. The optimal effort and aggregate supply of poached fish is:

$$\frac{d\Pi}{dE} = 0 \Rightarrow E^* = \max \left(0, \frac{s\sigma x - W_1}{2W_2}\right) \quad (\text{A.3})$$

$$\Rightarrow q^* = \max \left(0, \frac{s\sigma^2 x^2 - W_1 \sigma x}{2W_2}\right) \quad (\text{A.4})$$

Given the linear quadratic nature of the costs, there is no effort or catch for low stock levels and/or low prices. Effort and catch increase with the price paid to poachers,  $s$ .

## A.2 Traders as vertical monopolists, without farming

We introduce a trader who has market power on the end-market (monopoly) and on the primary market, making it a “vertical monopoly”. The trader has to set price  $s$  on the primary market to clear the poaching market. On the end market, we assume the trader faces a linear inverse demand :

$$P^m = \alpha^m - \beta^m q^W \quad (\text{A.5})$$

Trading an illegal commodity incurs transaction costs  $c$ . Hence, the monopoly profit can be written as :

$$\Pi^m = (\alpha^m - \beta^m q^W - c - s)q^W \quad (\text{A.6})$$

The optimal level of output is :

$$q_m^W = \frac{\alpha^m - c - s}{2\beta^m} \quad (\text{A.7})$$

Using the poachers' supply, it must be that in equilibrium, the supply of the

monopolist trader equals the supply of the poachers. The price paid to poachers  $s$  balances supply and demand (consistent with equation 13 in [Damania and Bulte \(2007\)](#)). Substituting  $s^*$  into equation A.7 yields the quantities of poached product in the vertical monopoly scenario :

$$\text{Price paid to poachers : } s_m^*(x) = \frac{W_2(\alpha_m - c) + \beta^m(W_1\sigma x)}{\sigma^2 x^2 \beta^m + W_2} \quad (\text{A.8})$$

$$\text{Poaching : } q_m^*(x) = \frac{\sigma^2 x^2 (\alpha_m - c) - W_1\sigma x}{2(\sigma^2 x^2 \beta^m + W_2)} \quad (\text{A.9})$$

First, note that equation A.9 is consistent with equation 14 in [Damania and Bulte \(2007\)](#), as the limiting case where  $W_1 = 0$  and  $W_2 = W$ .

### A.3 Captive breeding, imperfect competition and conservation

In this part of the model, a farmer can grow and sell totoaba. The theoretical model focuses on the duopolistic competition between the two actors on the end market for totoaba. As products are strategic substitutes, it is natural to investigate the case where Cournot competition arises. Indeed, when products are substitutes, each firm tries to maximize its residual demand (25). Nonetheless, given the asymmetric nature of costs, we also investigate Bertrand competition, as [Damania and Bulte \(2007\)](#).

**Introducing aquaculture :** the aquaculture farm needs to determine the optimal harvest age, based on the intrinsic growth rate in the pen, and expected prices. A sizeable literature has shown that rotation time is invariant to market structure in forestry applications ([Faustmann, 1849](#); [Mitra and Wan, 1986](#)) although quantities can be modified. The optimal rotation literature confirms the existence of a Faustmann rotation, where a set of  $T^*$  pens are equally distributed among each age class (1 pen per age class until  $T^*$ ). While it is arguably unrealistic to expect this structure for an inherited forest, it is reasonable to assume that a farm would *ex-ante* determine this rotation period given the expected price schedule over time. We assume that the aquaculture farm aims at producing a product that is as similar as possible from a biophysical stand-point and thus determines  $T^*$ . As we consider a stationary demand function, one can write the farming problem as a linear profit maximization problem, where the unit cost of production equals the capitalized sum of annual average variable costs over  $T^*$  periods. Therefore, we assume that an aquaculture firm can raise totoaba at cost  $v$  and sell it to the market:

$$\Pi^F = (P^F - v)q^F \quad (\text{A.10})$$

With  $v$  the unit cost per ton of totoaba, corresponding to the capitalized sum of annual costs.

**Utility maximization and demand functions :** upon the introduction of farmed goods, the inverse demand functions change. We use a model consistent with ([Singh and Vives, 1984](#)), where a representative consumer maximizes a quadratic and strictly concave utility function subject to prices:

$$\max_{q^W, q^F} V = \alpha^W q^W + \alpha^F q^F - \left( \frac{\beta^W (q^W)^2 + 2\gamma q^W q^F + \beta^F (q^F)^2}{2} \right) - p^W q^W - p^F q^F \quad (\text{A.11})$$

Two inverse demand functions emerge, that the traders and farmers face :

$$P^W = \alpha^W - \beta^W q^W - \gamma q^F \quad (\text{A.12})$$

$$P^F = \alpha^F - \beta^F q^F - \gamma q^W \quad (\text{A.13})$$

Where  $W, F$  refers to wild and farmed. We assume  $\gamma > 0$  e.g that goods are substitutes. When  $\alpha_W = \alpha^F$  and  $\beta^W = \beta^F = \gamma$ , the goods are perfect substitutes. When  $\alpha^F = \alpha^W$ , but  $\beta^F \neq \gamma$  or  $\beta^W \neq \gamma$ ,  $\frac{\gamma^2}{\beta^W \beta^F}$  measures the degree of product differentiation.

Rearrange the initial inverse demand functions into direct demand functions:

$$q^W = a^W - b^W P^W + e P^F \quad (\text{A.14})$$

$$q^F = a^F - b^F P^F + e P^W \quad (\text{A.15})$$

With  $a^i = \frac{\alpha^i \beta^j - \alpha^j \gamma}{\beta^i \beta^j - \gamma^2}$ ,  $b^i = \frac{\beta^j}{\beta^i \beta^j - \gamma^2}$  and  $e = \frac{\gamma}{\beta^i \beta^j - \gamma^2}$

**Cournot competition in the retail market:** assume that the two firms compete by setting their quantities. We solve the multi-stage game using backward induction. First, we derive the supply function resulting from Cournot competition. Second, we find the price paid to poachers so that the quantities supplied by the traders on the end market equal the quantities supplied by poachers.

Taking the inverse demand functions and plugging them into the profit functions:

$$\begin{aligned} \Pi^F &= (\alpha^F - \beta^F q^F - \gamma q^W - v) q^F \\ \Pi^W &= (\alpha^W - \beta^W q^W - \gamma q^F - s - c) q^W \end{aligned}$$

In a Cournot equilibrium, each firm takes its competitor's quantity as given, and picks optimal reaction functions.

Solving for the Nash equilibrium using reaction functions, each firm supplies:

$$\tilde{q}_c^W = \frac{2\beta^F(\alpha^W - (s + c)) - \gamma(\alpha^W - v)}{4\beta^W\beta^F - \gamma^2} \quad (\text{A.16})$$

$$\tilde{q}_c^F = \frac{2\beta^W(\alpha^F - v) - \gamma(\alpha^W - s - c)}{4\beta^W\beta^F - \gamma^2} \quad (\text{A.17})$$

Now, we find the equilibrium price paid to poachers for each unit of totoaba  $s_C^*(x)$  by equating  $\tilde{q}_c^W$  and  $q^W$ , and find the Nash equilibrium supply functions.

In the Cournot equilibrium:

$$\text{Price paid to poachers: } s_C^*(x) = \frac{2W_2(2\beta^F(\alpha^W - c) - \gamma(\alpha^F - v)) + W_1\sigma x(4\beta^F\beta^W - \gamma^2)}{4W_2\beta^F + \sigma^2x^2(4\beta^F\beta^W - \gamma^2)} \quad (\text{A.18})$$

$$\text{Poaching : } q_C^{W*}(x) = \frac{\sigma^2x^2(2\beta^F(\alpha^W - c) - \gamma(\alpha^F - v)) - 2\beta^F W_1\sigma x}{4W_2\beta^F + \sigma^2x^2(4\beta^W\beta^F - \gamma^2)} \quad (\text{A.19})$$

First, including a linear component for energy in the poaching cost significantly raises the price paid to poachers (when  $W_1 > 0$ ). Second, poaching decreases with the degree of substitutability between farmed and wild products ( $\gamma$ ), and increases with the production cost of farmed products  $v$ . On the other hand, it increases with demand for the wild product  $\alpha^W$ . For low stock values, poaching can be null since the production costs increase as stocks diminish. In the polar quadratic cost case (e.g.  $W_1 = 0$ ), our results differ from [Damania and Bulte \(2007\)](#) by a magnitude effect. Nonetheless, the results stand :

**Lemma 1:** *Assume the market is large, i.e., the residual demand for large stock levels is large enough. For any given wildlife stock, poaching levels in equilibrium with captive breeding will be lower than those without captive breeding, if the introduction of captive-bred animal products has no impact on the parameters of the original inverse demand function for wild animal products.*

See Appendix B.1. for proof of Lemma 1

### Bertrand competition in the retail market

**Interior solution:** the two firms compete by setting their prices. This section investigates a potential interior equilibrium, where both producers operate on the market.

Using demand functions instead of inverse demand functions:

$$q^F = a^F - b^F P^F + e P^W$$

$$q^W = a^W - b^W P^W + e P^F$$

With  $a^i = \frac{\alpha^i \beta^j - \alpha^j \gamma}{\beta^i \beta^j - \gamma^2}$ ,  $b^i = \frac{\beta^j}{\beta^i \beta^j - \gamma^2}$  and  $e = \frac{\gamma}{\beta^i \beta^j - \gamma^2}$

Firms set their prices. The Bertrand profit equations are :

$$\Pi^F = (P^F - v) q^F = (P^F - v)(a^F - b^F P^F + e P^W)$$

$$\Pi^W = (P^W - (s + c)) q^W = (P^W - (s + c))(a^W - b^W P^W + e P^F)$$

Solving for the reaction functions :

$$r^F(P^W) = \frac{a^F + b^F v + e P^W}{2b^F} \quad (\text{A.20})$$

$$r^W(P^F) = \frac{a^W + b^W(s + c) + e P^F}{2b^W} \quad (\text{A.21})$$

Finding the interior solution for the Nash Equilibrium :

$$P_B^F = \frac{2b^W(a^F + vb^F) + e(a^W + b^W(s + c))}{4b^F b^W - e^2}$$

$$P_B^W = \frac{2b^F(a^W + b^W(s + c)) + e(a^F + vb^F)}{4b^F b^W - e^2}$$

The equilibrium price paid to poachers is determined by equating the quantity supplied by the trader in Bertrand duopoly and the quantity supplied by the poachers and yields the quantity supplied yields :

### In the Bertrand equilibrium :

Price paid to poachers is :

$$s_B^*(x) = \frac{2W_2 b^W [b^F(2a^W + ev) + ea^F + c(e^2 - 2b^W b^F)] + W_1 \sigma x (4b^F b^W - e^2)}{\sigma^2 x^2 (4b^F b^W - e^2) + 2W_2 b^W (2b^F b^W - e^2)} \quad (\text{A.22})$$

Poaching is:

$$q_B^{W*}(x) = \frac{b^W [\sigma^2 x^2 (b^F(2a^W + ev) + ea^F + c(e^2 - 2b^W b^F)) - W_1 \sigma x (2b^F b^W - e^2)]}{2Wb^W (2b^W b^F - e^2) + (4b^F b^W - e^2) \sigma^2 x^2} \quad (\text{A.23})$$

We amend the original results from [Damania and Bulte \(2007\)](#) with the con-

curring Lemma 2:

**Lemma 2:** *With Bertrand competition, if the introduction of captive-bred products has no impact on the parameters of the demand function for wild animal products, poaching levels with captive breeding are ambiguous. The driver of the equilibrium is the cost ratio between aquaculture and the illegal poaching sector, i.e,  $v$  and  $c + s(x)$*

- For relatively low ratio values (i.e,  $c + s(x) \gg v$ ), poaching is unambiguously lower than without captive breeding for any given wildlife stock
- For intermediate ratio values, poaching is larger (for  $x < \tilde{x}$ ), then lower (for  $x > \tilde{x}$ ), than without captive breeding (with  $\tilde{x}$  such that  $q_B^{W*} = q_m^W$ )
- For large values of unit farming costs, poaching is unambiguously larger than without captive breeding for any wildlife stocks

See appendix B.2 for proof of Lemma 2.

Our results significantly differ from [Damania and Bulte \(2007\)](#), as Bertrand competition does not unambiguously lead to more extraction. Indeed, poaching functions are ambiguously ranked, and the final location of the steady state depends on the species intrinsic growth rate  $r$  and carrying capacity  $K$ .

With low farming costs, traders have an incentive to maintain large stocks. As the price paid to poachers is inversely related to the size of the stock, low harvest maintains large stocks and thus limits the price paid to poachers. Given its operational costs, it is the only way for the trader to remain competitive with the farming sector. On the other hand, when farming costs are large, the traders are incentivized to harvest more, as they can afford to pay a larger price to poachers while remaining competitive with the farming sector.

**Corner solution:** in a perfectly substitutable framework, a corner solution emerges if one firm has a lower marginal cost than the other: if farmed and wild animal products were perfect substitutes and farmed products unambiguously cheaper to produce, poaching would cease. In the context of imperfectly substitutable goods, this result is challenged. For poaching to cease, it must be that :

$$v = -\frac{1}{e}(2(a^W - cb^W) - \frac{1}{b^F}(ce + a^F)) \quad (\text{A.24})$$

In our setup, the marginal cost of production for farming would need to be **negative** for poaching to stop<sup>1</sup>. Moreover, as substitutability increases, this cost lowers. The relative cost of trading poached goods plays a minor role.

#### A.4 Steady state equilibria

Given the inverted U-shape of the logistic growth function, several steady-state equilibria can arise. First, if the *harvest function* (that is increasing and concave) is *steeper* than the growth function at low stock levels, there can be (i) no equilibrium if the harvest at  $K/2$  is larger than the growth rate, (ii) one bifurcation point (tangent harvest and growth functions at  $K/2$ , and (iii) two equilibria, with one stable and one unstable. If the *growth function* is *steeper* than the growth function at low stock levels, there can be (i) a single equilibrium, (ii) a bifurcation point and an equilibrium, (iii) three interior equilibrium, with only two being stable (see figure 4.2 for an illustration)

#### A.5 Extensions

**An oligopoly model:** we extend our model to gauge the impact of the number of traders and farmers. We denote by  $\mathcal{I}$  the set of individual traders  $i \in \mathcal{I}$  and by  $\mathcal{J}$  the set of individual farmers  $j \in \mathcal{J}$ . The demand functions are :

$$P_k^W = \alpha^W - \beta^W \sum_{i \in \mathcal{I}} q_i^W - \gamma \sum_{j \in \mathcal{J}} q_j^F \quad (\text{A.25})$$

$$P_l^F = \alpha^F - \beta^F \sum_{j \in \mathcal{J}} q_j^F - \gamma \sum_{i \in \mathcal{I}} q_i^W \quad (\text{A.26})$$

**Cournot oligopoly :** each farmer and trader maximizes profits by taking as given its competitors' quantity commitments. We assume traders and farmers are homogeneous, i.e for each type of producer, costs are identical :

$$i, j \in \mathcal{I}, i \neq j, c_i = c_j = c$$

$$k, l \in \mathcal{J}, k \neq l, v_k = v_l = v$$

Assuming that  $\text{card}(\mathcal{I}) = N$  and  $\text{card}(\mathcal{J}) = M$ , the profit functions for each farmer and trader can be written as :

$$\Pi_i^W = \left( \alpha^W - \beta^W(N-1)q_i^W - \beta^W q_i^W - \gamma M q^F - s - c \right) q_i^W \quad (\text{A.27})$$

$$\Pi_k^F = \left( \alpha^F - \beta^F(M-1)q_k^F - \beta^F q_k^F - \gamma N q^W - v \right) q_k^F \quad (\text{A.28})$$

---

<sup>1</sup>If consumers enjoy a numeraire good, they must receive compensation to consume the farmed good such that they increase their numeraire consumption to make up for the imperfectly substitutable nature of the farmed good.

Where  $q_i^W$  denotes the quantities sold by all other traders different from trader  $k$  (and  $q_l^F$  for farmers different from farmer  $l$ ). Given that all players in each type are identical cost-wise, the reaction functions are :

$$\forall i, j \in \mathcal{I} : q_i^W = q_j^W = q^W = \frac{\alpha^W - (s + c) - \gamma M q^F}{(N + 1) \beta^W} \quad (\text{A.29})$$

$$\forall k, l \in \mathcal{J} : q_k^F = q_l^F = q^F = \frac{\alpha^F - v - \gamma N q^W}{(M + 1) \beta^F} \quad (\text{A.30})$$

The **Cournot-Nash equilibrium** is :

$$\text{Poaching} : q_{\text{Cournot}}^W = \frac{\beta^F(M + 1)(\alpha^W - (s + c)) - \gamma M(\alpha^F - v)}{\beta^W \beta^F (M + 1)(N + 1) - \gamma^2 NM} \quad (\text{A.31})$$

$$\text{Farming} : q_{\text{Cournot}}^F = \frac{\beta^W(N + 1)(\alpha^F - v) - \gamma N(\alpha^W - (s + c))}{\beta^W \beta^F (M + 1)(N + 1) - \gamma^2 NM} \quad (\text{A.32})$$

$$(\text{A.33})$$

The primary market (between poachers and traders) must clear, and  $s(x)$  equates supply and demand:

$$N q_{\text{Cournot}}^W = q^W \quad (\text{A.34})$$

$$\iff s^{C^*}(x) = \frac{2W_2 N [\beta^F(M + 1)(\alpha^W - c) - \gamma M(\alpha^F - v)]}{\Omega} \\ + \frac{W_1 \sigma x (\beta^F \beta^W (M + 1)(N + 1) - \gamma^2 NM)}{\Omega} \quad (\text{A.35})$$

Where  $\Omega = \sigma^2 x^2 [\beta^F \beta^W (M + 1)(N + 1) - \gamma^2 NM] + 2W_2 N (M + 1) \beta^F$ . Solving for the equilibrium quantity, the quantity supplied on the market by individual traders is :

$$q_{\text{Cournot}}^W = \frac{\sigma^2 x^2 [\beta^F(M + 1)(\alpha^W - c) - \gamma M(\alpha^F - v)] - \sigma x W_1 N (M + 1) \beta^F}{\sigma^2 x^2 (\beta^F \beta^W (M + 1)(N + 1) - \gamma^2 NM) + 2W_2 N (M + 1) \beta^F} \quad (\text{A.36})$$

In our case study, when  $c = 0$ , it shows that when the number of farmers is larger than the number of traders, the introduction of farming generates larger steady-state stocks. An interesting perspective is when there remains 1 sole trader, and the number of farmers increases: in this case, poaching is drastically cut down, as shown in Figure 4.A. When the number of traders is larger than the number of farmers, steady-state stocks decrease. In our context, when the number of traders is limited, increasing the number of farming facilities is a safe way to guarantee conservation outcomes.

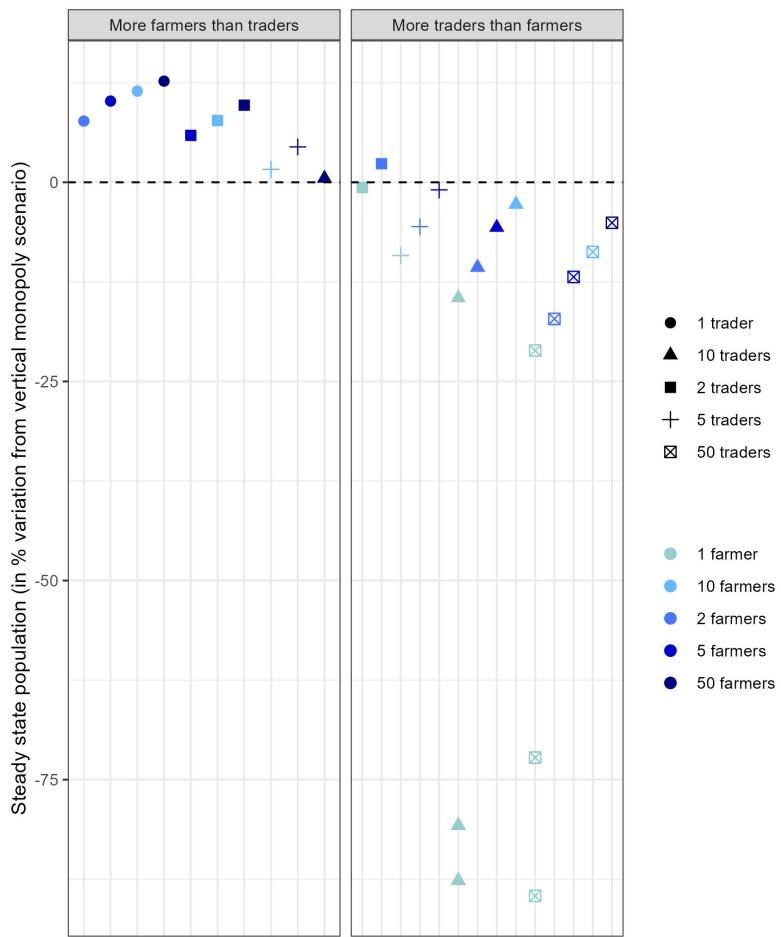


Figure 4.A: Steady state outcomes when multiple traders and multiple farmers are considered (an oligopoly) in the quantity adjustment scenario.

The left panel shows the steady state of the wild *Totoaba macdonaldi* population when there are more farmers than traders. The right panel shows the steady state of the wild population when there are more traders than farmers

**Bertrand oligopoly :** using the same notations as previously, the demand functions can be written as :

$$\forall i \in \mathcal{I} : q_i^W = q^W = \frac{1}{N}(a^W - b^W P^W - eP^F) \quad (\text{A.37})$$

$$\forall j \in \mathcal{J} : q_j^F = q^F = \frac{1}{M}(a^F - b^F P^F - eP^W) \quad (\text{A.38})$$

Using these demand functions and solving for the reaction functions in each case yields :

$$r^F(P^W) = \frac{a^F + b^F v + eP^W}{2b^F} \quad (\text{A.39})$$

$$r^W(P^F) = \frac{a^W + b^W(s + c) + eP^F}{2b^W} \quad (\text{A.40})$$

These reaction functions are the same as in the duopoly case (see eq. A.21). This result shows that aggregate production is invariant to the number of farmers or

traders as long as both are present on the market. Moreover, the individual production for traders is  $\frac{1}{N}q_B^W$  and  $\frac{1}{M}q_B^F$  with  $q_B^W$  and  $q_B^F$  referring to the duopoly equilibrium quantities for poached and farmed productions. In a Bertrand equilibrium, irrespective of the number of players, price-setting competition pushes the price to its minimum such that both firms still operate (given that traders have a stock-dependent production cost). Increased competition in the form of more players cannot push the prices further down. Therefore, aggregate output remains the same and individual production is divided among players.

This result further contradicts the results in [Damania and Bulte \(2007\)](#), as the authors find that increasing the number of players in a Bertrand set-up has detrimental effects on the steady-state stock. We find no effect, consistent with the theory and intuition.

**Trader take-over of the aquaculture sector :** in this section, we look at the 'extended cartel' scenario, where the vertical monopoly takes over the ownership of the aquaculture firm.

To gain intuition, assume poached and farmed products are perfect substitutes. On the one hand, the vertical monopoly has two production technologies: poaching (with a variable marginal cost, as the price paid to poachers depends on the population stock) and farming (with a constant marginal cost). In this case, the vertical monopoly equates the marginal costs across production units; that is, it buys a poached product to poachers up until the marginal cost of an extra poached unit equates to that of a farmed unit. In this case, if the marginal cost of farming is lower than market prices absent farming, then poaching goes down. Notice that the only way for traders to limit the price paid to poachers is to maintain a healthy stock. Therefore, the new equilibrium population stock is larger than the initial stock, and poaching is lower.

Now consider the case at stake, where products are imperfect substitutes. In this case, the extended cartel does not only equate marginal costs, as marginal revenues diverge across products. We use the following model to investigate the resulting equilibrium. Let the profit of the extended cartel be:

$$\Pi(q^F, q^W) = (\alpha^W - \beta^W q^W - \gamma q^F - (s + c))q^W + (\alpha^F - \beta^F q^F - \gamma q^W - v)q^F \quad (\text{A.41})$$

The extended cartel maximizes its profit with respect to the poached and farmed products. The poached production it sells on end markets is :

$$q^W = \frac{\sigma^2 x^2 (\beta^F(\alpha^W - c) - \gamma(\alpha^F - v)) - W_1 \beta^F \sigma x}{2(\beta^F W + \sigma^2 x^2 (\beta^F \beta^W - \gamma^2))} \quad (\text{A.42})$$

Figure 4.B shows that if the 'extended cartel' scenario arises, poaching goes

down, and the steady-state population increases.

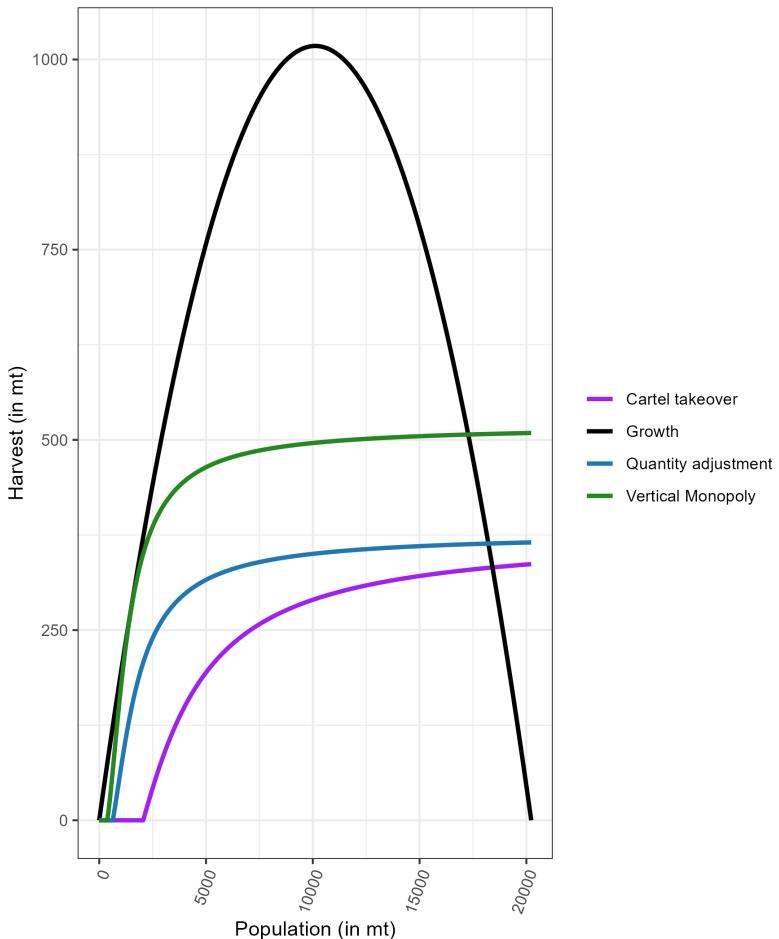


Figure 4.B: Steady-state equilibrium for the wild stock of *Totoaba macdonaldi* in the ‘extended cartel’ scenario, where the vertical monopoly takes over the ownership of farming operations

## B Proofs to lemmas

### B.1 Lemma 1 : content and proof

Assume  $\alpha^W = \alpha^m$  and  $\beta^m = \beta^W$ , i.e., that the demand faced by the monopolist is the same as in the duopolistic case. Comparing monopoly and Cournot harvest functions:

$$\begin{aligned} q_m^W &\geq q_c^W \\ \Rightarrow v &\leq \bar{v} = \alpha^F - \frac{\gamma(\alpha^m - c)\sigma^2 x^2 - W_1\sigma x}{2\beta^m\sigma^2 x^2 + 2W} \end{aligned}$$

First, look at when  $x \rightarrow 0$  :

$$\lim_{x \rightarrow 0} \bar{v} = \alpha^F$$

This requires that farming costs are lower than the choke price for consumers on their market. This condition is necessary for a farm competitor to enter the market.

Second, acknowledge that the second part of the equation is weakly decreasing, but non-increasing. Assuming the carrying capacity goes to infinity, it is limited by :

$$\lim_{x \rightarrow \infty} \bar{v} = \alpha^F - \gamma \frac{(\alpha^m - c)}{2\beta^m}$$

As fish abundance increases, the price paid to poachers decreases, as there is less scarcity. From equation (A.18), when  $x \rightarrow \infty$ , the price paid to poachers drops to 0. Moreover, notice that the last term in parenthesis is equation (A.7) for  $s = 0$ . Therefore, it means that the residual willingness to pay, when the poachers behave like a monopoly and  $x \rightarrow \infty$ , is larger than the unit cost of farming.

If the market is truly duopolistic, in the sense that the poachers could not manage the stock such that they depress demand so much as to kick their competitor out of the market, then Cournot competition unambiguously leads to lower poaching levels than a monopoly does.

## B.2 Lemma 2

Assume that the demand parameters are unchanged by the introduction of farmed substitutes, that is to say  $\alpha^W = \alpha^m$  and  $\beta^W = \beta^m$ , and use the definition of the coefficients for the direct demand function:

$$\begin{aligned} a^j &= \frac{\alpha^j \beta^i - \alpha^i \gamma}{\beta^j \beta^i - \gamma^2}; & b^j &= \frac{\beta^i}{\beta^j \beta^i - \gamma^2} \\ a^m &= \frac{\alpha^m}{\beta^m}; & b^m &= \frac{1}{\beta^m} \end{aligned}$$

For  $i, j \in \{W, F\}$  and  $m$  the monopoly case. To establish Lemma 2, we compare  $q_B^W$  and  $q_m^W$ . Equation (A.9) can be rewritten as :

$$q^m(a^m, b^m) = \frac{\sigma^2 x^2 (a^m - b^m c) - b^m W_1 \sigma x}{2\sigma^2 x^2 + 2W b^W}$$

Therefore:

$$\begin{aligned} q_m^W &\geq q_B^W \\ \Rightarrow v &\leq \frac{a^m - b^m c}{b^W b^F e} \left[ \frac{2W_2 b^W (2b^F b^W - e^2) + (4b^F b^W - e^2) \sigma^2 x^2}{2\sigma^2 x^2 + 2b^m W_2} \right] - \\ &\quad \frac{W_1 \sigma x [(4b^F b^W - e^2)(b^m - b^W) + e^2 b^W]}{b^W b^F e (2\sigma^2 x^2 + 2b^m W_2)} - \\ &\quad - \frac{e a^F + c(e^2 - 2b^W b^F) + 2b^F a^W}{b^F e} \end{aligned}$$

Notice that this equation can be reframed as :

$$F(x|c) \geq v \text{ where } F(x|c) = \Phi \frac{\eta + \mu x^2}{\theta + \nu x^2} - \frac{\kappa x}{\omega x^2 + \epsilon} - \zeta$$

And :

$$\Phi = \frac{a^m - b^m c}{b^W b^F e}, \eta = 2W_2 b^W (2b^W b^F - e^2), \mu = (4b^W b^F - e^2) \sigma^2,$$

$$\theta = 2W_2 b^m, \nu = 2\sigma^2, \zeta = (ea^F + c(e^2 - 2b^W b^F) + 2b^F a^W)$$

$$\kappa = \frac{W_1 \sigma [(4b^F b^W - e^2)(b^m - b^W) + e^2 b^W]}{b^F * e},$$

$$\omega = 2b^W b^F e \sigma^2 \text{ and } \epsilon = 2b^m b^W b^F e W_2$$

**Analysis of  $\Phi \frac{\eta + \mu x^2}{\theta + \nu x^2}$ :** if  $\mu\theta - \nu\eta < 0$ , the first component of  $F(x|c)$  is decreasing:

$$(4b^W b^F - e^2)b^m - 2(b^W b^F - e^2)b^W < 0$$

$$\iff \frac{\gamma^2}{\beta^m (\beta^W \beta^F - \gamma^2)^3} [\beta^m \beta^F + \gamma^2 - 4\beta^F \beta^W] < 0$$

Under the assumption that  $\beta^m = \beta^W = \beta^F = \beta$ , it is clear that

$$\frac{\gamma^2}{\beta(\beta^2 - \gamma^2)} (\gamma^2 - 3\beta^2) < 0$$

as  $\gamma < \beta$ . Therefore,  $\Phi \frac{\eta + \mu x^2}{\theta + \nu x^2}$  is decreasing  $\forall x$

**Analysis of  $\frac{\kappa x}{\omega x^2 + \epsilon}$**  : the second component of  $F(x|c)$  is increasing for  $x \leq \sqrt{\frac{\epsilon}{\omega}}$ , and decreasing after, since  $x \in \mathbb{R}^+$ . Noticing that  $\kappa < 0$ :

- For  $x \in [0, \frac{1}{\sigma} \sqrt{W_2 b^m}]$ ,  $\frac{\kappa x}{\omega x^2 + \epsilon}$  is negative and decreasing
- For  $x > \frac{1}{\sigma} \sqrt{W_2 b^m}$ ,  $\frac{\kappa x}{\omega x^2 + \epsilon}$  is negative and increasing

**Conclusion :** overall,  $F(x|c)$  is such that :

- For  $x \leq \frac{1}{\sigma} \sqrt{W_2 b^m}$ , the first component is decreasing, while the second component is increasing
- For  $x \geq \frac{1}{\sigma} \sqrt{W_2 b^m}$ , the first component is decreasing and the second component is decreasing

Hence,  $F(x|c)$  is bounded above by  $\max(F(0|c), F(\frac{1}{\sigma}\sqrt{W_2 b^m}|c))$ , and bounded below by  $F(K|c)$  where  $K$  is the system carrying capacity. Therefore:

1. If  $v < F(K|c)$ , then Bertrand harvest is always lower than monopoly harvest
2. If  $F(K|c) < v < F(0|c)$ , then Bertrand harvest starts by being lower than in the monopoly case, but gets larger for large stock values.
3. Eventually, if  $F(0|c) < v$ , then Bertrand harvest is always larger than in the monopoly case

Figure 4.C illustrates this lemma with our parameter specification.

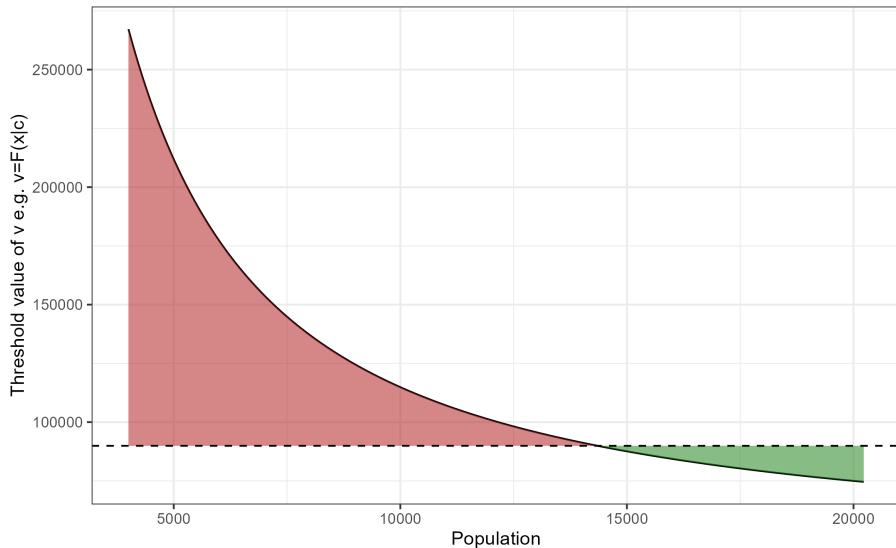


Figure 4.C: Evolution of the threshold  $v$  to compare vertical monopoly and price setting (Bertrand) harvest functions

In green, vertical monopoly harvests more than in the price setting equilibrium. For larger population values, in red, price setting leads to more harvest than the vertical monopoly. This illustrates our main specification and property 2 above.

**Corner equilibrium:** for a corner solution to emerge, it must be that  $q_B^{w*} = 0$ ,

$$v = v(x) = \frac{W_1(2b^F b^W - e^2)}{\sigma x b^F e} - \frac{2b^F a^W + ea^F + c(e^2 - 2b^W b^F)}{b^F e} \quad (\text{A.43})$$

Equation A.43 shows that for low stock values, costs can still be positive and poaching disappear. However, to ensure that poaching is *never* beneficial in the Bertrand equilibrium, it must be that  $v = \min v(x) = -\frac{2b^F a^W + ea^F + c(e^2 - 2b^W b^F)}{b^F e}$ . In this case, the subsidy rate is so high that production is always beneficial for the farmer, and prices are too low for the trader to compete. In our baseline specification, this would amount to  $v = -720,855$  USD.

## C Supplementary Figures and Tables

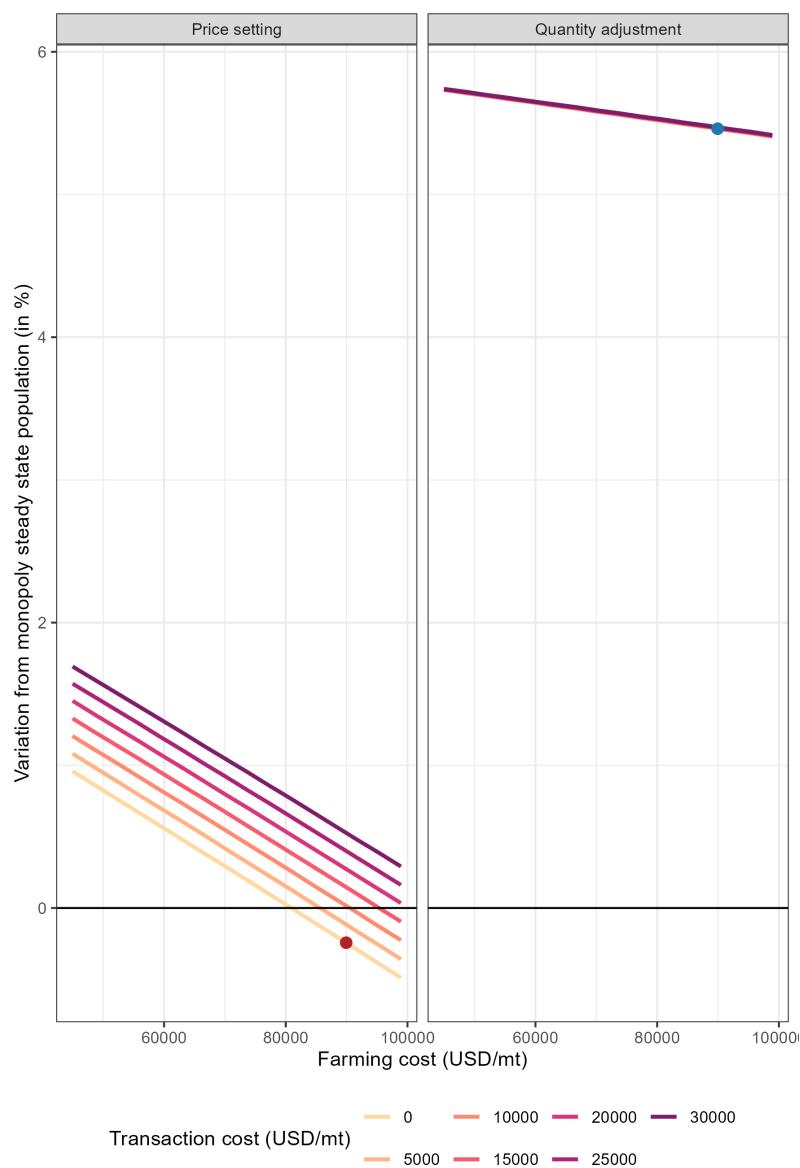


Figure 4.D: Percent change in steady state population across scenarios, following the joint evolution of illegal transaction and farming costs

Red and blue dots represent baseline results in the price setting and quantity adjustment scenarios

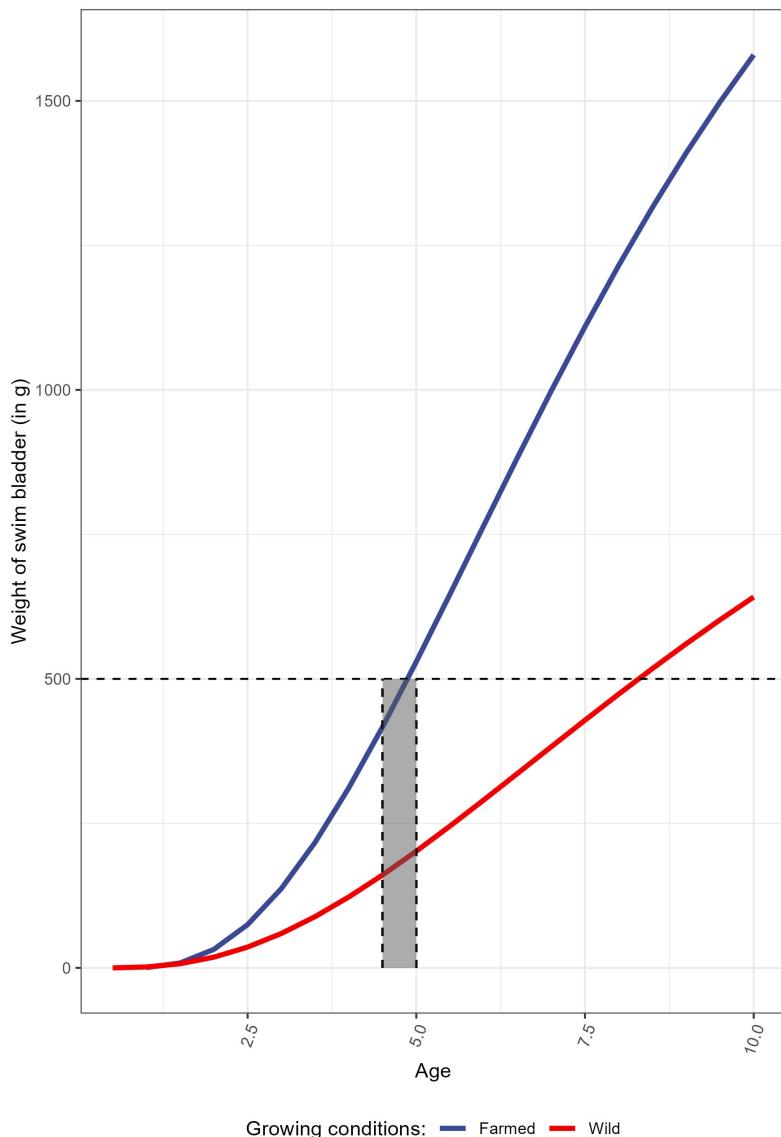


Figure 4.E: Von Bertalanffy Growth curves for wild and farmed *Totoaba macdonaldi* under different growing conditions

Gray box indicates the range of ages that possess a 500 gram swim bladder. The wild individual growth curve was calibrated with information from the stock assessment, while the farmed individual growth curve was calibrated using

Variable	Low Season	Mid Season	High Season	Source
Vessels	5	20	50	<a href="#">Cisneros-Mata (2020)</a>
Days per month	4	12	14	<a href="#">Cisneros-Mata (2020)</a>
Total fleet days year	20	240	700	<a href="#">Cisneros-Mata (2020)</a>
Food fuel day	525	525	525	Semi-Structured Interviews
Totoaba gearset	2	3	6	<a href="#">Cisneros-Mata (2020)</a>
Gear loss day	0.5	0.5	0.5	Semi-Structured Interviews
Gearset vessel per day	2	3	3	<a href="#">Cisneros-Mata (2020)</a>
Gear replacement	1600	1600	1600	Semi-Structured Interviews
Bribes/year	600	7200	21000	Semi-Structured Interviews
Average cost (per vessel day)	8385.34	14386.69	5051.26	Authors' calculation

Table 4.F: Supporting information for the calculation of the *Totoaba macdonaldi* poaching cost parameters ( $W_1$  and  $W_2$ )

The methods section details how and when semi-structured interviews were conducted.

<i>Dependent variable:</i>	
	Price
Catch	-1,563.752** (725.985)
Constant	1,625,837.000*** (406,789.500)
Observations	45
R <sup>2</sup>	0.097
Adjusted R <sup>2</sup>	0.076
Residual Std. Error	431,737.700 (df = 43)
F Statistic	4.640** (df = 1; 43)

Note: \*p<0.1; \*\*p<0.05; \*\*\*p<0.01

Table 4.G: Regression output for the linear demand estimation calculated by regressing price data on catch data.

Data were obtained from the available literature that provided estimated weight and value of *Totoaba macdonaldi* maw seizures on estimated *Totoaba macdonaldi* catch from 2014 to 2017 obtained from a recent stock assessment. The methods section details where information was obtained from.

Variable	Value	Source
Sphere	1.00	Earth Ocean Farm Video, 2022
Capacity per sphere (t)	144.00	Earth Ocean Farm Video, 2022
<i>In \$USD</i>		
Maintenance year	12500.00	Felipe Ramirez, InnovaSea, 2018
Cleaning year	5000.00	Felipe Ramirez, InnovaSea, 2018
Vessel maintenance/year	10000.00	Tyler Korte, BlueOcean Mariculture, 2018; Fernando Cavalin, Earth Ocean Farms, 2018
Fuel year	25122.50	Author's Calculations
Feed	312480.00	Tyler Korte, BlueOcean Mariculture, 2018
Labor	1580000.00	Authors' calculations
Facility lease	150000.00	Cygnus Ocean Farms, 2017
Admin.	50000.00	Cygnus Ocean Farms, 2017
Operational costs	2145102.50	Authors' calculations
Operational costs (per t & year)	14896.55	Authors' calculations

Table 4.H: Supporting information for the calculation of the *Totoaba macdonaldi* farming cost parameter ( $v$ )

Annual cost estimates were obtained from informants and converted to \$USD. Capacity of each farming pen was obtained from Earth Ocean Farms, and an annual cost 706 per tonne of totoaba was calibrated using personal communications with totoaba aquaculture producers.

Parameter	Value	Concept	Units
$\alpha$	1,625,836.98	Demand model : intercept	USD
$\beta$	1,563.75	Demand model : coefficient	USD/metric ton of biomass
$\gamma$	1,354.25	Demand model : substitutable good coefficient	USD/metric ton of biomass
$r$	0.20	Intrinsic growth rate	unitless
$K$	20,226.00	Carrying capacity (in metric tons)	metric tons of biomass
$\sigma$	$2 \times 10^{-5}$	Catchability	% of biomass/vessel trip
$AvgCost$	14,386.69	Average cost per vessel trip at historical value	USD/vessel trip
$W$	3.75	Quadratic cost parameter - Quadratic cost function	USD vessel trip <sup>-2</sup>
$W_1$	12200.00	Linear cost parameter - Linear quadratic cost function	USD/vessel trip
$W_2$	0.57	Quadratic cost parameter - Linear quadratic cost function	USD vessel trip <sup>-2</sup>
$v$	89929.92	Unit cost of farming	USD/metric ton of biomass
$i_r$	0.10	Interest rate	%
$Age$	4.50	Age of farmed totoaba	Years
$c$	0.00	Unit cost of trading	USD/ metric ton of biomass

Table 4.I: Summary of *Totoaba macdonaldi* ecological and market parameters for model calibration

The methods section details where information was obtained to estimate each parameter, as well as relevant equations.

Concept	Formula	Reference
<i>Fishery</i>		
Growth	$\dot{x} = rx(1 - \frac{x}{K}) - \sigma xE$	eq. A.2
<i>Poaching</i>	$s$ is price paid to poachers	
Harvest technology	$q = \sigma xE$	
Profit	$\Pi = s \times (\sigma xE) - W_1 E - W_2 E^2$	
Poached harvest	$q^W = \frac{s\sigma^2 x^2 - W_1}{2W_2}$	eq. A.4
<i>Vertical monopoly scenario</i>		
Demand	$P^m = \alpha^m - \beta^m q$	eq. A.5
Profit	$\Pi^m = (P^m - s - c)q$	eq. A.6
Supply on end market	$q_m^*(x) = \frac{\sigma^2 x^2 (\alpha_m - c) - W_1 \sigma x}{2(\sigma^2 x^2 \beta^m + W_2)}$	eq. A.9
<i>Duopoly</i>		
Aquaculture profit	$\Pi^F = (P^F - v)q^F$	eq. A.10
Demand for imperfect substitutes	$P^W = \alpha^W - \beta^W q^W - \gamma q^F$	eq. A.12
	$P^F = \alpha^F - \beta^F q^F - \gamma q^W$	eq. A.13
Quantity adjustment (Cournot) supply	$q_C^{W*}(x) = \frac{\sigma^2 x^2 (2\beta^F (\alpha^W - c) - \gamma (\alpha^F - v)) - 2\beta^F W_1 \sigma x}{4W_2 \beta^F + \sigma^2 x^2 (4\beta^W \beta^F - \gamma^2)}$	eq. A.19
Price setting (Bertrand) supply	$q_B^{W*}(x) = \frac{b^W [\sigma^2 x^2 (b^F (2\alpha^W + ev) + ea^F + c(e^2 - 2b^W b^F)) - W_1 \sigma x (2b^F b^W - e^2)]}{2W b^W (2b^W b^F - e^2) + (4b^F b^W - e^2) \sigma^2 x^2}$	eq. A.23

Table 4.J: Summary of the key functions in the model

For model conclusions, the plotted functions are growth, vertical monopoly end market supply ( $q^m$ ), quantity adjustment end market supply ( $q_C^W$ ) and price setting end market supply ( $q_B^W$ )

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# Conclusion

This dissertation explores the bioeconomic modeling of biodiversity loss, addressing two key questions: (1) How do endogenous spatial processes impact the drivers of biodiversity decline, and how can they be managed to mitigate this decline? (2) What role does strategic behavior play in exacerbating or alleviating these drivers, and how can bioeconomic models account for these behaviors to inform effective conservation policies?

By combining insights from both economic theory and ecology, this dissertation contributes to the vast body of literature that seeks to develop integrated approaches to biodiversity, bioeconomic modeling. Through a combination of spatial models, dynamic optimization, and strategic behavior analysis, the research presented here offers both theoretical and practical insights into how biodiversity can be conserved in a complex and interconnected world.

## Managing endogenous spatial processes

In chapter 2, the research focuses on the tension between managing space for conflicting objectives, particularly the trade-off between reducing wildfire risk and conserving biodiversity habitat. Forest patches display dynamic successional stages - each forest patch grows through time -, contributing to both fire risk and biodiversity, depending on their spatial arrangement. Their absolute and relative location in space, e.g. own characteristics and the degree to which they are connected to neighboring patches matter for connectivity. The study reveals that managing habitat and wildfire risk within landscapes is inherently complex due to the non-convexity of the underlying connectivity : the successional stage and location relative to neighbors crucially matters. I demonstrate that under certain conditions, it is possible to maintain habitat connectivity while limiting wildfire risk, but this balance becomes precarious in the face of climate change, or with limited policy budgets.

This chapter confirms results from existing studies in terms of the production possibility frontier between habitat and wildfire risk (Calkin et al., 2005), the decreasing marginal efficiency of treatments (Wei et al., 2008; Yemshanov et al., 2022) and provides an interpretative framework using graph theory for existing results (Minas et al., 2014; Rachmawati et al., 2016; Konoshima et al., 2008;

[Yemshanov et al., 2021](#)).

This contribution is significant in that it highlights how spatially dynamic features - specifically, the centrality of certain patches within a network - affect the efficacy of conservation efforts. Managing central nodes, which have outsized impacts on the connectivity of the landscape, proves to be a critical factor in reducing risk when habitat connectivity is not a policy priority. However, when it is, treatments should focus on less central patches, and their number should gradually diminish. Graph theory provides an effective framework to understand the location of treatments at a small scale. This chapter also provides a methodological insights relative to the scalability of small scale results. In small graphs, connectivity metrics tend to be very correlated. Hence, information from small landscapes provides limited information for large scale policy design.

However, the research also demonstrates that the non-convex nature of spatial connectivity of habitat and wildfire patches complicates optimization. Traditional methods, particularly those that rely on linear or convex assumptions, continuity, or limited numbers of variables such as dynamic programming, fail to provide optimal solutions in the high-dimensional, discrete space of ecological management. In this context, the dissertation introduces the use of heuristics and approximations to manage complexity, though at the cost of reducing the planning horizon and the analytical tractability of the model.

Chapter 3 extends this analysis to the management of invasive species, where the strategic deployment of ecological fences is examined along with *in situ* control policies. The chapter revisits a model of mobile public goods ([Costello et al., 2017](#)), and makes connectivity both a tool and a challenge for managing pests. The findings show that optimal connectivity can be designed to contain invasive species effectively : redirecting the flow of pest species to where it is best controlled, or least invasive is welfare enhancing. This changes the results of previous models ([Costello et al., 2017](#)) that treated connectivity as exogenous to the system. By treating connectivity as a decision variable, this research provides new insights into how species can be controlled more efficiently through spatial interventions. However, the decentralized management of connectivity complicates matters: in some cases, suppressing a spatial externality, such as species spread, can leave spatial arbitrage opportunities untapped, where heterogeneity across the landscape could have been leveraged for better ecological and economic outcomes.

Both chapters emphasize the importance of considering spatial dynamics and connectivity in conservation strategies. However, these chapters highlight an incompatibility frontier for current bioeconomic models ([Levin et al., 2013](#)). Increasing the number of state variables (e.g. considering more interrelated spa-

tial units), incorporating temporal dynamics (increasing the planning horizon), and representing complex ecological interactions (non-convexities in aggregate landscape connectivity, decisions which depend on the state variables) lead to complex problems at the frontier of research. In this case, analytical tractability is difficult to maintain. Hence, including these layers of mathematical complexity changes the purpose of models: while many models were first and foremost heuristic, building fictitious worlds to glean insights on specific policy issues, they become more prescriptive and predictive ([Varenne, 2014](#)) and their heuristic role is challenged.

## The role of strategic behavior in biodiversity management

The second major theme of this dissertation is the impact of strategic behavior on biodiversity management, explored in Chapters 3 and 4. In Chapter 3, the strategic behavior of landowners in the management of connectivity and invasive species is examined. The findings reveal that when landowners act in their own interest - overfencing their properties to prevent the spread of invasive species - spatial fragmentation results. This defensive strategy tends to internalize the damages of invasive species, but prevents the full exploitation of spatial heterogeneity in the landscape, where different patches could serve as containment zones for invasive species at lower management costs. The chapter illustrates that when actors fail to consider the broader ecological benefits of coordinated action, they miss opportunities to improve both ecological and economic outcomes. Overfencing not only leads to inefficient use of resources but also hinders the natural movement of species that could have been managed more effectively through strategic, coordinated interventions.

In Chapter 4, the dissertation turns to the strategic behavior of actors within market systems, focusing on the case of the *Totoaba macdonaldi*, an endangered species targeted by poaching. The chapter reveals that vertical monopolies do not necessarily lead to overharvesting or resource depletion. Instead, the relationship between upstream and downstream actors - particularly the constraints imposed by downstream producers - can limit the extent of overexploitation. As fishing becomes more costly when stocks decrease, this puts a bound on the capacity of the vertical monopoly to supply large quantities while maintaining its margin, on top of classical demand related constraints related to its elasticity. Moreover, Bertrand competition, often expected to lead to aggressive overharvesting ([Bulte and Damania, 2005](#); [Damania and Bulte, 2007](#)), is tempered by these same constraints. Contrary to existing results, we show that Bertrand competition does not necessarily lead to market flooding and stock collapse. The introduction of conservation aquaculture offers a viable solution to poaching, provided that farming

costs remain low and poaching penalties are enforced. In a second best world, where a fishing ban is difficult to enforce, and property rights are difficult to assign, leveraging *de facto* property rights and designing smart market conditions may provide a better alternative than increasing law enforcement.

This analysis underscores the importance of considering strategic interactions in biodiversity management, whether in spatially explicit contexts, as in Chapter 3, or within market structures, as in Chapter 4. In both cases, strategic behavior complicates the optimization of conservation outcomes but also offers opportunities for leveraging market or spatial incentives. By recognizing and incorporating strategic behavior into bioeconomic models, policymakers can design interventions that account for the realities and consequences of human behavior in both conservation and market systems.

## Policy implications

The findings of this dissertation suggest several important policy recommendations. First, for wildfire and habitat management, spatial optimization can guide treatment operation, and the dynamic appraisal of landscapes should be in the landplanner's toolbox. Allocating resources to central nodes - those patches with the greatest influence on landscape connectivity - will help maximize the benefits of fuel treatment interventions. However, when biodiversity habitat is factored in, the careful design of biodiversity corridors is key, and graph theoretical procedures can help. Although our results suggest that current network centrality measures fail to be leveraged on large scales, research development in centrality metrics can considerably increase the efficiency of multi-objective fuel treatments.

Second, in the management of mobile public bards ([Costello et al., 2017](#)), policymakers should focus on coordinated connectivity control rather than allowing decentralized actors to overfence their regions. Policies should focus on optimal ecological network design, where temporary fencing and containment policies can achieve larger welfare improvements than control alone. There is no one-size-fits-all policy recommendation when heterogeneity is factored in. Nonetheless, information on the distribution of costs and biological productivities should guide optimal fencing policies: if large costs zones have low biological productivity or stock, they should be isolated, to avoid either contaminating other patches or receiving inward dispersal, which comes at substantial costs. To conclude, this article goes in the direction of spatially explicit, incentive compatible policies to form coalitions for service provision such as agglomeration bonuses ([Parkhurst et al., 2002; Bareille et al., 2023](#)).

Third, in the context of conservation farming and poaching, the case of *Totoaba macdonaldi* suggests that market-based solutions can play a pivotal role in reduc-

ing pressures on wild populations. Subsidies for aquaculture, combined with demand reduction campaigns, and sustained law enforcement against poaching, can help tip the balance toward sustainable conservation outcomes. In settings where property rights are difficult to assign and regulate, and local law enforcement is difficult, the use of command and control approaches like trade bans under CITES may not be efficient. Using market based instruments such as trade ban exemptions can be a tool to curb poaching. Policymakers must also consider the market structure when designing interventions, as both monopolistic and competitive dynamics affect the incentives for conservation. Policy design at the collective level can use insights from imperfectly competitive market structures such as totoaba's. As a matter of fact, these structures can be welfare enhancing compared to *status quo*, result in decreased fishing effort, increased biomass and increased (tax) revenues ([Englander and Costello, 2023](#)).

## Limitations and future research

While this dissertation provides valuable insights, it also faces several limitations. In chapter 2, I use a bounded dynamic vegetation model to maintain the possibility to analyze integrally the set of initial conditions. In doing so, I restrict the potential states of the world and the depiction of the relationship between wildfire risk, habitat suitability, and successional stage. Therefore, increasing the temporal depth of the model is as much of concern as increasing the scale, to allow for different fire-habitat-successional stage relationships and better guide policy. Additionally, including economic heterogeneity in the costs of treatment and potential damage would benefit policy making. Finally, centrality measures are shown not to scale well on larger graphs. We believe insights from the small scale results are valid, but the relevant large scale centrality measures, and additional computational experiments, are required to sustain that claim. Therefore, avenues for future research involve different approaches to build robust information about the temporal and spatial location of treatments. I plan on sampling medium to large scale location and solve the repeated and dynamic optimization procedures with genetic algorithms. Second, using the results from this first step optimization procedure, I plan on characterizing the solution using graph theoretical networks and training neural networks to recognize optimal treatment patterns, and help guide larger scale optimization procedures.

In chapter 3, I so far restricted the analysis to 2 players, and the endogenous formation of a 2 node graph. Further analysis implies increasing the number of players to really study the emergence of complex network structures, where the structuring into components (e.g. disconnected subgraphs) may emerge as optimal policy options, displaying positive connectivity within component. In do-

ing so, I would like to study the properties of efficient policies, how they shape ecological-economic network, and how graph theoretical measures can help dealing with complex optimization problems.

In chapter 4, our policy recommendations build on uncertain economic and ecological data, as ecological data is expensive to get, and illegal market data difficult to encounter. Data scarcity on ecological processes is a key feature of bioeconomic modeling. In my future research, I want to integrate more data sources from ecology, especially at a fine spatial resolution, including products from satellite imagery and Geographic Information Systems (GIS). With these limitations in mind, our policy recommendations should be taken cautiously.

Additionally, several additional layers could be included. First, we do not acknowledge for dynamic pricing interactions, where the stockpiling of swim-bladders is an option to increase prices through time, as we expect on-the-ground seizures to remain a threat. However, these effects have been shown to matter ([Kremer and Morcom, 2000](#)), and further analysis is required. Second, we restrict our analysis to specific fish behavior, where fish do not have specific migratory routes or spawning grounds, and thus, the catch decreases proportionally to population size. One fruitful research avenue is to enhance the set of fish school behaviors considered in the model, such as stock hyperstability (i.e. when costs of fishing do not increase as the population decreases, because fish tend to group at specific locations, for mating processes for example), to test the validity of our policy recommendations.

Future research avenues are both methodological and thematic. In order to grasp the intricacies of the drivers of biodiversity loss drivers, I want to study how to increase the total complexity of models, by refining the aspects I traded for others among chapters.

Increasing the spatial resolution of models hinders the use of traditional dynamic optimization techniques, such as dynamic programming ([Bellman, 1957](#)). While techniques are being developed to increase the spatial resolution of models and limit their computational burden ([Brumm and Scheidegger, 2017](#)), these techniques may not be sufficient. Systems of ordinary differential (or difference) equations can be more convenient to solve, but partial differential (or difference) equations ([Brock and Xepapadeas, 2010, 2020](#)) systems allow spatial variables to be considered in a continuous way (e.g. 1, 2 or 3 dimensions) and can be of interest to study large spatial issues.

The non-convexities identified in the spatial models, particularly in Chapter 2 (and likely present in the development of chapter 3 as network size is increased) present significant challenges for scaling these models to real-world applications. In my future research, I want to explore ways to develop scalable optimization

methods that can handle the complexity of spatial dynamics without sacrificing computational efficiency. Machine learning offers a promising avenue for addressing these challenges by enabling the development of more flexible, high-dimensional models, such as statistical learning and scaling up from heuristic optimization methods applied to medium size landscapes.

Another limitation is the lack of stochasticity in the models presented. Real-world ecological processes are subject to a wide range of uncertainties - random species invasions, wildfire ignitions, and market fluctuations, among others. Incorporating stochastic elements into the models would provide a more robust foundation for making policy recommendations that can withstand the unpredictability of ecological and economic systems. However, as stated earlier, this level of complexity triggers operational research problems, where the solvability of such models is difficult. The climate macroeconomics literature has developed tools to incorporate large spatial scale modeling with stochastic processes into optimization frameworks ([Cai et al., 2020](#); [Fernández-Villaverde et al., 2024](#)), thus paving the way for similar approaches for biodiversity economics.

As biodiversity decline is a multispecies and multiscale phenomenon, future research should expand beyond the single-species models used here to consider multi-species interactions and community-level approaches. Conservation efforts should focus not only on minimizing economic "bads," such as invasive species, but also on optimizing the broader ecological landscape, including the provision of Nature's Contributions to People (NCPs). Indeed, the management of connectivity should not only be apprehended through the hardships of mobile public bads, or single species habitat suitability but also through the lense of other biodiversity contributions. For example, in the case of species providing positive NCPs, ecological connectivity is of great value, as it provides insurance against stochastic population variation ([Loreau et al., 2003](#)). While habitat-based models provide a basis for such endeavor, the analysis of population dynamic for species with different habitat requirements raises issues regarding the choice of spatial scale to aggregate different species, and compare patches.

In this dissertation, I have shown that bioeconomic models serve as a platform for the analysis of biodiversity through its ecological and economic lense, in a trully interdisciplinary fashion. Gradually, they have been refined to encompass advances from both economics and ecology. As they are models with a mathematical formulation, their resolution is made difficult with increasing complexity, and analytical tractability vanishes. With data being scarce, they can be difficult to calibrate, but increases in both ecological and economic dataset availability at a fine temporal and spatial resolution are changing calibration issues. I firmly believe that this method is suited for the challenges of the future. Data driven methods are perfect for analyzing the past, but may fail to predict the future.

In the context of the ecological crisis, developing models to understand, predict, and guide policy making is paramount. As I want to continue studying landscape connectivity and its value, other approaches are complimentary. This thesis cruelly lacks original empirical evidence on the value of connectivity. This strand of my research is burgeoning, and modern causal inference methods can be used to analyze changes in the value of connectivity, as they have been recently used to understand the value of individual species (Frank, 2024; Frank and Sudarshan, Forthcoming). The literature on the estimation of spillover effects of policy in environmental and epidemiological systems is a lively field and has provided great methodological and empirical contributions (Deschenes and Meng, 2018; Reich et al., 2021). The literature focuses on the causal estimation of treatment effects with known (or assumed dispersal) patterns. Chapters 2 and 3 highlight that shocks to parameters such as growth, economic costs and damages can have far reaching consequences in terms of network structure : shocks not only have impacts on local populations, but also on the structure of the network and the pattern of spillovers. Recent advances in econometrics (Comola and Prina, 2021) foster new ways to understand changes relative to landscape connectivity with endogenous changes in spillovers.

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