

# Forward and inverse modelling of eco-evolutionary dynamics

in biological and economic systems



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# Summary

Biological and economic systems are complex adaptive systems, composed of multiple organisms and entities in interaction, themselves experiencing evolutionary processes. Interaction and evolutionary processes operate at different organizational scales, from genes to ecosystems and from individual behavior rules to national economies, generating complex couplings across scales. Yet, despite this astonishing organizational complexity, biological and economic systems both display invariant patterns. The latter originate from general organizational principles, and the study of ecological and economic systems deals with identifying them.

Recently, studies have shown that evolutionary processes can occur on similar time scales as ecological processes, generating eco-evolutionary feedbacks which may play an important role on the dynamics of biological systems. Also, in economic systems, studies are suggesting that economic change is determined by analogous eco-evolutionary processes. Yet, our understanding of eco-evolutionary processes and feedback mechanisms in empirical systems is limited, because of the over simplicity of current eco-evolutionary models and the lack of confrontation with empirical data. Developing novel modelling approaches to improve the modelling of empirical systems, this thesis aims at advancing our general understanding of eco-evolutionary processes and feedbacks shaping the dynamics of biological and economic systems.

Specifically, ?? presents and analyses an eco-evolutionary model on spatial graphs to understand how eco-evolutionary processes, together with complex habitat structures, influence the phenotypic distribution of biological populations. ?? presents an inverse modelling framework to estimate the most likely parameter values of dynamical models from empirical data, permitting to discriminate between competing eco-evolutionary hypotheses. ?? test whether processes operating on economic activities, comprising positive and negative interactions between them, their spatial dispersal and their transformations, can explain their dynamics at the country level. To reach this goal, the inverse modelling framework, together with data covering 59 years of economic time series over 74 countries, are used. Finally, ?? presents two numerical methods to efficiently simulate eco-evolutionary models of biological populations structured in high dimensional spatial and phenotypic spaces.

Together, this thesis advances our general understanding on the eco-evolutionary processes and feedbacks shaping the dynamics of biological populations and economic activities. A holistic map of elemental eco-evolutionary feedbacks influencing spatially structured biological populations is established. As regards economic systems, processes involving positive interactions between economic activities, and their spatial dispersal, are evidenced to systematically affect their dynamics at the country scale. In parallel to those fundamental results, novel forward and inverse modelling methods are developed, allowing to better capture the dynamics of empirical systems. In the face of the ongoing climate and biodiversity

crisis, it is of urgent to accelerate our general understanding of the mechanisms shaping our world. Bridging biology, mathematical modelling, machine learning and economics can massively help us to reach this goal.

## Résumé

Les systèmes écologiques et économiques sont des systèmes complexes adaptatifs, composés d'organismes hétérogènes et d'entités en interaction, eux-mêmes affectés par des processus évolutifs. Les processus d'interactions et d'évolution opèrent à différents niveaux d'organisation, des gènes aux écosystèmes et des règles de comportement individuel aux économies nationales, générant des couplages d'échelles. Pourtant, malgré cette incroyable complexité, les systèmes écologiques et économiques démontrent tous deux des comportements invariants. Des mécanismes d'organisation généraux sont à l'origine de ces derniers, et l'enjeu principal de l'étude des systèmes écologiques et économiques est de les identifier.

Récemment, des études ont montré que certains processus évolutifs peuvent agir à des échelles de temps similaires à celles des processus écologiques, donnant alors lieu à des boucles de rétroaction éco-évolutives qui pourraient jouer un rôle fondamental sur la dynamique des systèmes écologiques. Par ailleurs, dans les systèmes économiques, des études suggèrent que le changement économique est déterminé par des processus éco-évolutifs analogues. Néanmoins, notre compréhension des processus éco-évolutifs et des boucles de rétroaction dans les systèmes empiriques est limitée, du fait de la simplicité des modèles actuels, et à cause du manque de confrontation avec des données empiriques. Développant de nouvelles approches visant à mieux modéliser les systèmes empiriques, cette thèse a pour objectif d'avancer dans notre compréhension générale des processus et boucles de rétroaction façonnant la dynamique des systèmes écologiques et économiques.

Le ?? présente et analyse un modèle éco-évolutif sur graphes spatiaux pour comprendre comment des processus éco-évolutifs, en concert avec des structures d'habitat complexes, influencent la distribution phénotypique de populations biologiques. Le ?? présente une méthode de modélisation inverse pour estimer la valeur la plus probable de paramètres de modèle dynamiques à partir de données empiriques, permettant de distinguer différentes hypothèses éco-évolutives. Le ?? teste si des processus s'appliquant aux activités économiques, comprenant des interactions positives et négatives entre elles, leurs dispersions spatiales et leurs transformations, peuvent expliquer leur dynamique à l'échelle d'un pays. Dans ce but, la méthode de modélisation inverse, ainsi que des données économiques couvrant 59 années dans 74 pays, sont utilisées. Finalement, le ?? présente 2 méthodes numériques permettant de simuler des modèles éco-évolutifs de populations biologiques structurées dans des espaces géographiques et phénotypiques de grande dimension.

Cette thèse fait progresser notre compréhension générale des processus et boucles de rétroaction éco-évolutifs impliqués dans la dynamique de populations biologiques et dans

celle des systèmes économiques. Une carte des boucles de rétroaction éco-évolutives affectant les populations biologiques structurées est établie. De même, il est démontré que des interactions positives entre les activités économiques, et leur dispersion spatiale, affectent considérablement et de façon généralisée leur dynamique à l'échelle d'un pays. En parallèle de ces résultats fondamentaux, de nouvelles méthodes de simulation et de modélisation inverse sont présentées, permettant de mieux rendre compte des dynamiques de systèmes empiriques. Face à la crise climatique et de la biodiversité en cours, il est urgent d'accélérer notre compréhension générale des mécanismes qui affectent notre monde. L'association de disciplines telles que la biologie évolutive, la modélisation mathématiques, l'apprentissage machine et les sciences économiques peut nous y aider de façon substantielle.



# Acknowledgement

What a journey! Four years ago, I have decided to embark on a ship to live a big adventure. Worryingly lacking sailing experience, I still envisioned a voyage in unknown seas, at the crossroads between biology, economics, and applied mathematics. I wanted to experience storms and dangers because, as Alfred Maufray said, "*À vaincre sans périls, on triomphe sans joie*" (**maufrais1997aventures**). But honestly, I was not expecting so much! Here are some words that cannot express all the gratitude I have towards these people who supported me all along this journey, and without whom I could not have made it safe back home.

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# Introduction

„ Nature loves to hide.

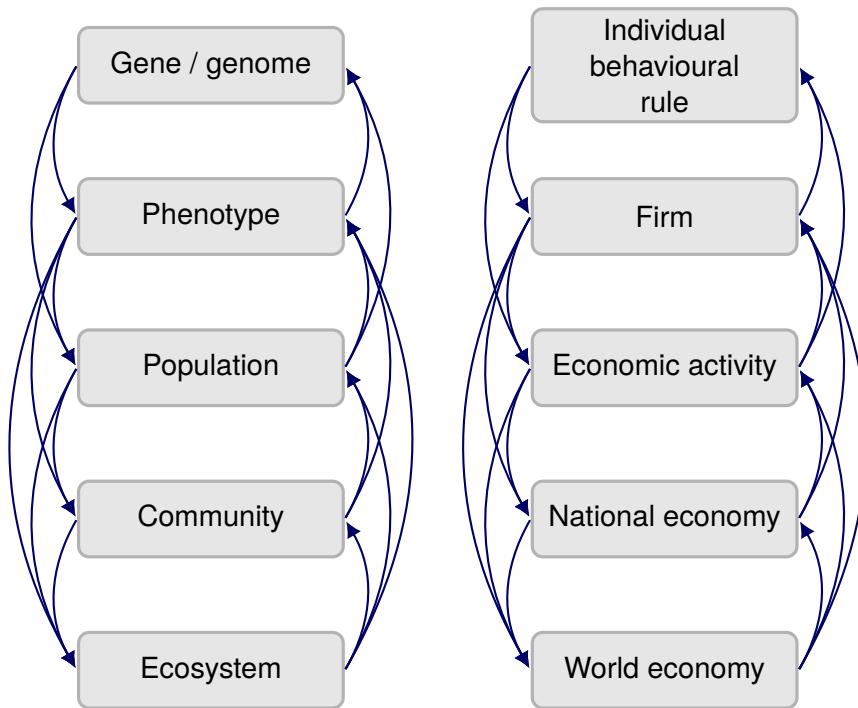
— Heraclitus (c.6th-5th century BCE)

## 1.1 Context

### 1.1.1 Biological and economic systems as complex adaptive systems

What are the similarities between the dynamics of biological and economic systems? Think of a biological system as a community of interacting biological organisms (Chapin et al., 2002), and think of an economic system as a community of interacting economic agents (Dopfer and Potts, 2007). The dynamics of a biological system depends on fluxes of matter and energy between organisms, and the dynamics of an economic system depends on fluxes of capital between economic agents. *A priori*, the underlying processes strongly differ, because the behavior of economic agents is motivated by rationality, where economic agents maximize utility (Lawson, 2013). Nonetheless, economic agents are faced with uncertainty (Foster and Metcalfe, 2012) and their rationality is bounded (Veblen, 1898; Nelson, 1985). As a result, economic agents adopt a variety of behavioral rules (e.g. technological, organizational, institutional, see Foster and Metcalfe, 2012) through trial-and-errors, which are subject to natural selection through competition processes (Schumpeter, 2017). In this perspective, both biological and economic systems are complex adaptive systems (Levin, 2002), composed of heterogeneous entities that interact in nonlinear ways and experience evolutionary processes. The processes of interaction and evolution involved take many forms and operate at different organizational level (Levin, 1998), from genes to ecosystems, and from organizational routines to economies, with feedback mechanisms between the organizational levels (see Fig. 1.1). Interestingly, the stochasticity of the processes involved, and their couplings, do not necessarily lead to unpredictable structures and dynamics, but rather induce organized structural properties and invariant patterns (Olff et al., 2009; Mitchell, 2009). In biological systems, invariant patterns include patterns of species richness, where for instance montane regions are often associated with a disproportionately high number of species (Rahbek et al., 2019b). In economic systems, invariant patterns include the bimodal shape of the distribution of international income, where some countries have systematically developed much more rapidly than others (Acemoglu et al., 2001). A common direction on the research agenda in biology and economics is to understand general organizational principles, i.e. to underpin the fundamental processes and feedbacks that generate invariant

patterns (Levin, 2002; Olff et al., 2009; Veldhuis et al., 2018). In biological systems, the fundamental processes resulting in patterns of species richness are identified (Rahbek et al., 2019a; Rangel et al., 2018; Hagen, 2022), and the current challenge is to underpin the mechanisms resulting from their couplings (Hagen, 2022). In economic systems, we still do not exactly understand the fundamental processes at stake.

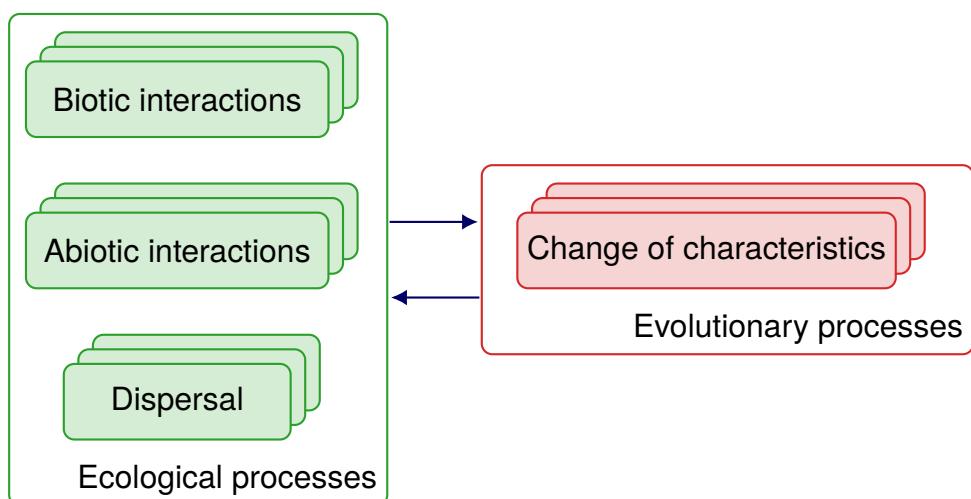


**Fig. 1.1:** Graphical representation of organizational levels and their couplings in biological and economic systems. An arrow indicates that the organizational level at its tail can influence the organizational level at its head. Left diagram is inspired from Hendry, 2016.

### 1.1.2 Ecological and evolutionary processes drive the dynamics of biological systems

In biological systems, interaction processes are more commonly designated as ecological processes, and encompass the processes of interaction between organisms (biotic interactions) and between organisms and their environment (abiotic interactions), as well as dispersal processes (movement of individual across space) (Vellend, 2010, see Fig. 1.2 for a graphical representation). Evolutionary processes designate those processes responsible for the change of heritable characteristics (DNA, genes, phenotypes) over successive generations ((Hall, 2013), Fig. 1.2). The coupling between ecological and evolutionary processes is acknowledged since the very birth of the theory of evolution. During his voyage on the Beagle, Darwin documented a link between the different ecological opportunities across the Galápagos Islands and the different beak shapes in the finches he found on each island (Dar-

win, 1859). He reasoned that the variations in ecological opportunities lead to a differential in survival for certain phenotypes, which over time resulted in the evolution of different beak shapes. Since then, we know that ecological processes interact with evolutionary processes, and they together shape the long term dynamics of biological systems (Rahbek et al., 2019a; Rangel et al., 2018; Hagen, 2022). Empirical studies have now demonstrated that evolution can be rapid and occur on similar time scales as ecology (Hairston et al., 2005; Pelletier et al., 2009) and have quantifiable effects on ecological dynamics (Ezard et al., 2009), leading to feedbacks between ecological and evolutionary processes, so-called eco-evolutionary feedbacks (Pelletier et al., 2009; Schoener, 2011; Govaert et al., 2019). Eco-evolutionary feedbacks involve situations where an ecological process (e.g., replication, competition, dispersal) influences an evolutionary process (e.g. phenotypic change), which then feeds back to an ecological process, or vice versa (Govaert et al., 2019, Fig. 1.2). Examples are feedbacks between population dynamics (replication and competition) and phenotypic change, which can lead to evolutionary branching through the effect of competition (Dieckmann and Doebeli, 1999). In spatially structured populations, another classical example of eco-evolutionary feedbacks is the mechanism of local adaptation (Savolainen et al., 2007), where feedbacks between population dynamics, dispersal and trait evolution can facilitate or prevent populations to adapt to local environmental conditions (Meszéna et al., 1997; Doebeli and Dieckmann, 2003). Importantly, the eco-evolutionary feedbacks involved in adaptation mechanisms are expected to affect the dynamics of ecosystems in the coming decades (Norberg et al., 2012; Urban et al., 2016), because of the expected rapid changes in environmental conditions due to anthropogenic pressure and climate change (Ellis, 2011; Midgley and Hannah, 2019). Nevertheless, our understanding of eco-evolutionary feedbacks in realistic biological scenarios is limited (Lion et al., 2022).



**Fig. 1.2:** Graphical representation of the eco-evolutionary processes determining eco-evolutionary dynamics in biological. By extension, I use this terminology to designate interaction and evolutionary processes in economic systems.

### 1.1.3 Drivers of economic change

In economic systems, the fundamental processes determining economic change are controversial (Dopfer and Potts, 2007; Nelson et al., 2014; Hodgson, 2019). To explain economic development, the neoclassical theory (Lawson, 2013) assumes that economic systems are in equilibrium, in the sense that the demand and supply of goods and services are balanced on all relevant markets. Firms are rational in maximizing profits by adapting to demand and supply, and the observed economic change is driven by exogenous forces, such as technological change (Romer, 1986). Evolutionary economics, promoted by the seminal work of Nelson et al., 2014, criticizes this view and seeks to explain economic change by focusing on endogenous forces. Evolutionary economics suggests that interactions between economic agents, firms and economic activities, and evolutionary processes acting upon them, are major processes contributing to economic change (Hodgson, 2019). These interactions may consist in facilitation processes through supply chains (Ozman, 2009; Saavedra et al., 2009; Van Der Panne, 2004) or competition within markets (Wernerfelt, 1989). What determine these interactions, and firm and economic activities' behavior in general, are organizational routines (Fig. 1.1), which spread across space and adapt (Cordes, 2006), affecting economic development at the local, regional, national, and international scale. Because these proposed processes are analogous to eco-evolutionary processes driving the dynamics of biological systems (which motivates the use of this terminology for designating economic processes in the following), a number of modelling approaches have borrowed concepts and methods from biology, aiming at underpinning the fundamental processes underlying invariant patterns in economic systems (Tacchella et al., 2018; Saavedra et al., 2009; Scholl et al., 2021; Zhang et al., 2018; Modis, 1997; Saavedra et al., 2014; Farmer and Lo, 1999; Michalakelis et al., 2011; Marasco et al., 2016; Gatabazi et al., 2019; Cauwels and Sornette, 2012; Applegate and Lampert, 2021; Suweis et al., 2015). For instance, (Saavedra et al., 2009) has successfully used a model of mutualistic interaction to explain structural patterns in industrial cooperation. Also, Scholl et al., 2021 uses the concepts of food webs and density dependence to explain market malfunctions and excess volatility in financial markets. However, those studies did not seek to understand how eco-evolutionary processes may affect economic development at the national scale. Biologically inspired eco-evolutionary models may help to disentangle the effect of eco-evolutionary processes on the dynamics of national economic systems, and could explain differences in economic development across countries.

## 1.2 Modeling eco-evolutionary dynamics

### 1.2.1 Forward modelling of eco-evolutionary processes

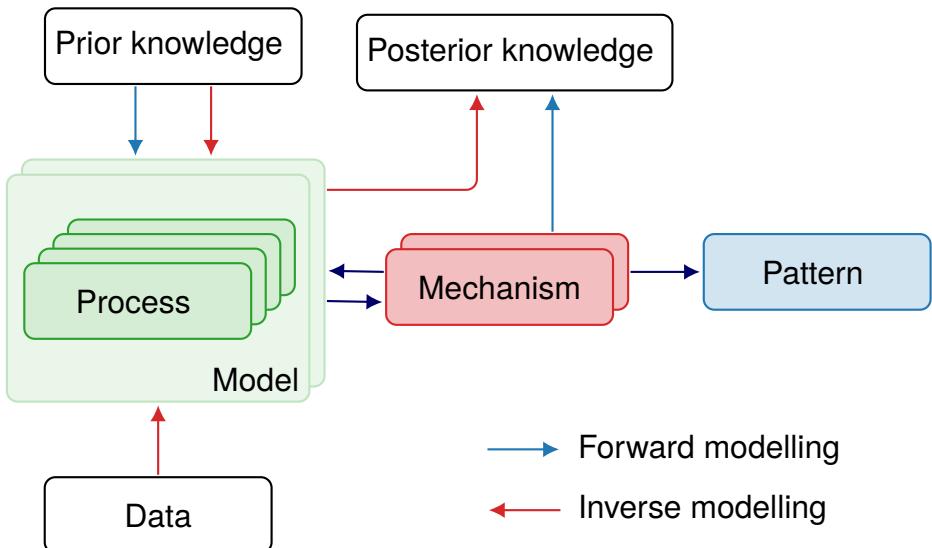
The complex interplay between ecological and evolutionary processes can hardly be studied with experimental approaches (Pontarp et al., 2019; Hagen, 2022, but see **Becks2012** for an experimental study with rotifer-alga microcosms). As such, a deductive approach, relying on forward modelling, has traditionally been put forward to underpin the mechanisms underlying invariant patterns in biological systems (Brummitt et al., 2020). Along this approach,

hypotheses about causal processes are embedded in a model, whose simulation (integration) generates emergent (non-anticipated) properties (see Fig. 1.3). Emergent properties may be seen as predictions from the consideration of the processes considered (May, 2004), and the role of the modeler is to underpin the underlying mechanisms, i.e. to disentangle how the interplay between the processes generate the observed behavior. In the early 1930s to 1940s, by formulating tractable mathematical models implementing the processes of reproduction, dispersal and mutations, the work of Fisher, Wright and Haldane has greatly contributed to the modern synthesis of evolutionary biology (Huxley and Others, 1942), generally accepted as the basis of our current understanding of evolutionary dynamics. Yet in order to obtain tractable mathematical model, Fisher, Wright and Haldane have neglected eco-evolutionary feedbacks (Govaert et al., 2019). In particular, ecological processes have been strongly simplified, and the effect of evolutionary processes on population dynamics has been neglected (Lion et al., 2022).

With the increase in computational capacity, novel modelling approaches relying on individual based models (IBMs) have appeared (DeAngelis and Mooij, 2005). These models require less simplifying assumptions than traditional mathematical models (DeAngelis and Mooij, 2005), and can unveil more realistic mechanisms by allowing to capture processes acting at the individual level. However, the lack of analytical tractability of IBMs is a shortcoming, because it challenges the ability of the modeler to underpin general principles from the simulations (Lion, 2016; May, 2004). The recent development of mathematical techniques, such as moment closure approximations (Law and Dieckmann, 1999; Gandhi et al., 2000; Nordbotten et al., 2020; Lion, 2016), adaptive dynamics theory (Metz et al., 1995), and probability theory (Champagnat et al., 2006), are generating novel pathways by filling the gap between IBMs and mathematical models. Analogous to renormalization group analysis developed in quantum and statistical physics (Sayama, n.d.), they form a toolbox to rigorously derive how emergent properties are influenced by processes operating at different organizational levels. As such, these mathematical techniques allow an analytical underpinning to IBM simulations, and can generate a general understanding of the key mechanisms at stake (Lion, 2016).

The combination of numerical simulations and, e.g., adaptive dynamics theory, has successfully shed new lights on the emergence of evolutionary branching under feedbacks between population dynamics and phenotypic change (Dieckmann and Doebeli, 1999; Doebeli and Dieckmann, 2003). An other example is the work of Meszéna et al., 1997; Débarre et al., 2013; Mirrahimi and Gandon, 2020, that has provided new insights on the effect of habitat heterogeneity on local adaptation. However, our current understanding of eco-evolutionary feedbacks neglects specificities of real biological populations that may significantly alter the resulting mechanisms, such as the structuration of populations over complex spatial structures (Nowak and Komarova, 2001) and highly dimensional phenotypic space (Doebeli and Ispolatov, 2010).

The consideration of such factors is important to advance our understanding, but raises challenging methodological issues. In particular, adding complexity in eco-evolutionary models may hinder the fundamental mechanisms underlying the emergence of a pattern. Also, the consideration of multiple traits leads to an increase in the dimensionality of the model, which in turn leads to an exponential increase in the computational cost associated to the



**Fig. 1.3:** Forward and inverse modelling approaches for the understanding of complex adaptive systems. A forward modelling approach consists in deriving a model, embedding a set of processes inspired from prior knowledge. The objective is to understand how the interplay between the processes considered transforms in (feedback) mechanisms that are associated with an invariant pattern. An inverse modelling approach integrates empirical observation within the modelling process. Posterior knowledge on the empirical system is obtained whether from the interpretation of the estimated parameter values, or through model selection.

numerical simulations (Bellman, 2010). In order to better understand eco-evolutionary dynamics, we need to investigate more realistic scenarios, which in turn require methodological developments, in order to cope with the extra complexity and computational cost.

## 1.2.2 Inverse modelling

Another approach to underpin processes and mechanisms in biological systems consists in inverse modelling, where empirical data is used to constrain the model (Clermont and Zenker, 2015, see Fig. 1.3 for a graphical illustration). Inverse modelling can take the form of parameter estimation (Schartau et al., 2017) or model selection (Johnson and Omland, 2004), both involving the use of inference methods to estimate, respectively, the most probable model parameter value, or the most probable model among candidates, given empirical data. In parameter estimation, provided that they are inferred together with uncertainties, parameters can be interpreted to better understand the strengths and effects of the processes considered (Pontarp et al., 2019). For instance, Higgins et al., 2010; Curtsdotter et al., 2019 infer the parameters of population dynamic models to understand the processes involved in ecosystem functions. In model selection, candidate models embedding competing hypotheses about causal processes are derived, and the relative support of each model given the data is computed to discriminate between the hypotheses (Johnson and Omland, 2004). For instance, using inverse modelling and alternative eco-evolutionary

models, (Skeels et al., 2022) shows that temperature-dependent evolutionary speed most likely explains variations in biodiversity patterns, among alternative evolutionary speed hypotheses.

The computation of the most probable model parameter values, or the computation of the different model supports, critically involves inference methods. Inference methods commonly demand many forward integration of the model, resulting in a computational cost that can be prohibitively expensive (Schneider et al., 2017). The number of forward integration required may dramatically increase with the number of model parameters (Csilléry et al., 2010), and the number of model parameters, together with the model nonlinearities, can eventually lead to false estimates of the most probable model parameter values (Gábor and Banga, 2015). Consequently, inverse modelling methods have mostly been used with simple evolutionary models (Csilléry et al., 2010). Eco-evolutionary models are dependent on numerous parameters (Boyd, 2012), are strongly nonlinear (Hastings et al., 1993; Huisman and Weissing, 1999; Benincà et al., 2008), and their integration is computationally expensive (Fisher et al., 2018), challenging the use of inverse modelling to underpin eco-evolutionary processes. Advances in the field of artificial intelligence could circumvent these issues, allowing to advance our knowledge of eco-evolutionary dynamics in empirical systems.

### 1.2.3 Artificial intelligence to leverage forward and inverse modelling

In the recent years, the field of artificial intelligence (AI) has made enormous progresses in computer vision (Voulodimos et al., 2018) and natural language processing (Young et al., 2018). At the backbone of this success are key computational techniques that could leverage the forward and inverse modelling of eco-evolutionary dynamics. Advances in computer vision and natural language processing rely on deep learning methods, that allow neural networks to learn abstract representation of mechanisms from large datasets (LeCun et al., 2015). These abstractions can hardly be interpreted to generate scientific theories (Karpatne et al., 2017), and their prediction ability is limited by the information contained in the training datasets. As such, neural networks cannot be used *per se* to gain scientific insights and extrapolate beyond observed trends (Barnosky et al., 2012; Urban et al., 2016). Nevertheless, their traditional applications and associated methods have been successfully derived in other scientific fields for this purpose (Kashinath et al., 2021; Schneider et al., 2017; Yazdani et al., 2020; Rolnick et al., 2022). Neural networks have been used to reduce the cost of the forward integration of climate models, learning more efficient representations of physical mechanisms (Kashinath et al., 2021). They have also been used to approximate the solution of partial differential equation (PDE) models (Sirignano and Spiliopoulos, 2018; Han et al., 2018), with the major advantage of approximating high dimensional problems at a lower computational cost than traditional methods. Underlying the training of neural network is the technique of backpropagation (LeCun et al., 2015). This technique can be generalised to train any scientific model against data (Rackauckas et al., 2020a), with the potential to leverage inverse modelling techniques (Frank, 2022). Consequently, AI techniques offer unique opportunities for advancing our understanding of eco-evolutionary dynamics.

## 1.2.4 Programming languages

Combining AI techniques with scientific models requires a computational environment that allows to easily develop scientific models, while ensuring simulation performance, and providing composability between AI and other scientific libraries (Rackauckas et al., 2020a). Unfortunately, performance and composability are features that are poorly represented in mainstream programming languages used by the scientific community, such as Python, Matlab or R. Those languages are naturally attractive because they are dynamically typed (Bezanson et al., 2017), allowing convenient development iterations. Nonetheless, prototypes written in Python, Matlab or R need to be rewritten in low level, compiled languages such as C, C++ or Fortran for speed and predictable mapping to hardware (Perkel, 2019; Bezanson et al., 2017). This conversion requires significant efforts, leading to a problem commonly designated as the "two-language problem" (Bezanson et al., 2017). In order to circumvent performance issues, most libraries in Python, Matlab or R rely on bindings with low level languages. For instance, the most used deep learning libraries in Python, TensorFlow and PyTorch, are internally written in C++ (see *Tensorflow* 2015; Foundation, 2016). However, bindings with low level languages come with major negative externalities. First, they restrict the understandability of their source code to computer scientists – prohibiting potential development contributions from the scientific community. Second, they prevent the composability of, e.g., traditional scientific computing libraries and deep learning libraries (Innes et al., 2019). This absence of composability arises because deep learning libraries must differentiate the numerical models to be trained. Yet, TensorFlow or PyTorch are only able to differentiate models written in their own internal source code (Innes et al., 2019).

Julia is a recently developed programming language that addresses the issue of the two-language problem (Bezanson et al., 2017; Bezanson et al., 2018). Julia was built over a type-specializing, just-in-time compiler, which makes it easy to generate performant programs in pure Julia, while preserving the essential features of Python, Matlab or R, such as dynamic typing and automatic memory management (Perkel, 2019). The source code of most Julia libraries is consequently written in pure Julia, guaranteeing understandability and composability. In particular, Julia is an automatic differentiation pervasive language (Innes et al., 2019), which allows to differentiate any model written in pure Julia without any modification. As a result, deep learning libraries can be used on any scientific model written in Julia (Rackauckas et al., 2020b). Solving the two-language problem, Julia permits scientists to prototype a program which is readily generic and performant, benefitting not only the development process but also the entire research community (Bezanson et al., 2017). Overall, the composability and productivity granted by Julia makes it an ideal computational environment to accelerate research.

## 1.3 Thesis outline

In summary, while it is increasingly acknowledged that feedbacks between ecological and evolutionary processes play an important role in biological systems (Pelletier et al., 2009; Urban et al., 2016), our understanding of eco-evolutionary dynamics in realistic scenarios is limited. Under increasing anthropogenic pressure, advancing this understanding is essential

(Urban et al., 2016) but raises challenging methodological issues. Further, while analogous processes to eco-evolutionary processes have been suggested to influence the dynamics of economic systems (Hodgson, 2019), we do not know their effect on economic dynamics at the scale of a country. Here, I present novel forward and inverse modelling approaches to advance our understanding of eco-evolutionary dynamics, and utilize them to shed light on the eco-evolutionary processes and feedbacks in biological and economic systems.

In ??, I investigate how eco-evolutionary processes, in combination with complex habitat structures, influence the phenotypic distribution of biological populations. I proceed using a forward modelling approach: I derive a stochastic eco-evolutionary IBM where individuals are structured over a spatial graph, and experience the fundamental processes of reproduction, competition, mutation and migration. Seeking to understand how those processes result in phenotypic differentiation at the population level, I derive analytical approximations of the IBM. Together with extensive numerical simulations, they provide insights into how the graph properties affect the population size and phenotypic differentiation. In particular, I show that three main graph properties, relating to landscape connectivity, heterogeneity in connectivity, and habitat spatial auto-correlation, shape phenotypic differentiation. These results establish mechanistic links between landscape features and the eco-evolutionary dynamics of biological populations.

In ??, I develop an inverse modelling method to estimate the parameters of eco-evolutionary models and perform model selection. The method is based on a machine learning framework and involves the combination of state-of-the-art AI techniques and a novel learning strategy. The learning strategy consists in training the model against mini-batches of data with short time horizon, which I analytically show to bypass problems arising from model nonlinearities. I implement the ML framework in a new Julia library released under the name of **MiniBatchInference.jl**, and demonstrate through numerical experiments that it can efficiently and accurately estimate model parameters and provide model support from noisy, incomplete and independent time series. Altogether, the proposed ML framework is a workhorse for inverse modelling and can elucidate mechanistic pathways in biological and economic systems.

In ??, I quantify the effect of eco-evolutionary processes on the dynamics of economic systems. I employ the ML framework developed in ?? to investigate how alternative eco-evolutionary population models can explain the dynamics of economic activities in 74 of the world's richest countries, relying on 59 year of economic data. The models embed processes acting upon economic activities, including ecological interactions between them, their spatial dispersal, and their transformation transformations. The statistical support of each model is compared to a simple logistic growth model, taken as a null model. I find strong statistical evidence for positive interactions between national economic activities, and spatial dispersal. To my knowledge, this is the first study providing quantitative evidences that eco-evolutionary processes shape the dynamics of economic systems.

In ??, I extend two recent methods to solve high dimensional non-local nonlinear PDEs. This class of PDEs can be used to construct generic eco-evolutionary models capturing the evolution of complex phenotypic populations, but up to now, could only be simulated in low dimensions. The first method presented relies on Picard iterations, while the second is based on deep learning and involves neural networks to approximate the PDE model

output. I implement both methods in the Julia library **HighDimPDE.jl**, and evaluate their performance on high dimensional eco-evolutionary models, and on PDE models arising in physics. The methods yield good results with short run times, opening up new venues to further our understanding of eco-evolutionary dynamics.

# Discussion

‘‘ *To be but one with all living things, to return, by a radiant self-forgetfulness, to the All of Nature.*

— Friedrich Hölderlin (1770-1843)

Understanding biological and economic systems involves the underpinning of general organizational principles at the origin of invariant patterns (Levin, 2002, Fig. 1.3). Aiming at advancing our understanding of eco-evolutionary dynamics in biological and economic systems, this thesis contributed to

- (i) a general understanding of the role of eco-evolutionary processes in shaping the dynamics of biological populations structured in complex landscapes (??),
- (ii) the quantification of the effect of eco-evolutionary processes on the dynamics of economic systems at the country level (??),
- (iii) methodological advances in the forward and inverse modelling of eco-evolutionary dynamics (??????).

In the following, I discuss the chapters of this thesis collectively within the broader context of their contribution to our current understanding of the dynamics of biological and economic systems, and how they advance the current eco-evolutionary modelling paradigm. I further highlight current limitations, and propose future research directions.

## 2.1 Contributions

### 2.1.1 Linking eco-evolutionary processes to patterns of differentiation

Phenotypic differentiation arises from feedbacks between population dynamics, dispersal and mutations (Hamilton, 2021), and ?? determines how these feedbacks are modulated by landscape features. Mutations act upon individual organisms, and result in genetic drift in finite size populations, causing stochastic variations in the allelic proportions and phenotypes of biological populations (Slatkin, 1987). In geographically structured populations, drift results in patterns of neutral differentiation (Slatkin, 1987), where isolated populations are characterized by differentiated allelic proportions and phenotypes. Dispersal tends to reduce neutral differentiation (Slatkin, 1987), and this effect is modulated by landscape connectivity (Wright, 1943; McRae, 2006; McRae and Beier, 2007) through the mechanism of "isolation by limited dispersal" (Orsini et al., 2013). By increasing the dispersal ability of organisms, landscape connectivity decreases neutral differentiation (Lande, 1991). When landscapes

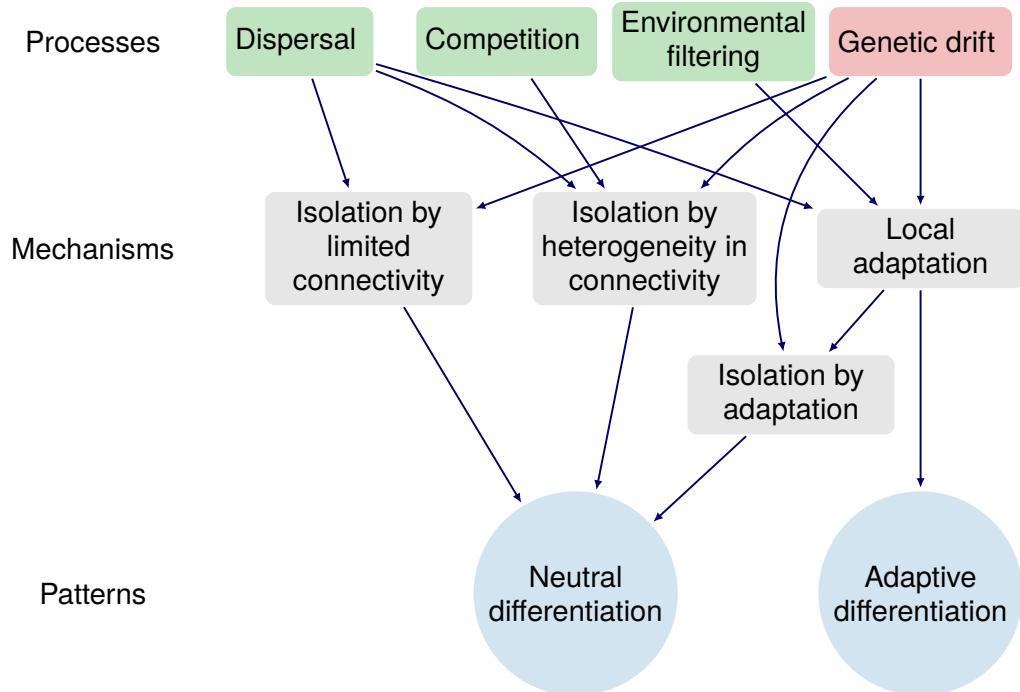
present heterogeneous habitats, natural selection can supplement the effect of genetic drift and increase the sole effect of stochasticity on differentiation ([fisher1958genetical](#)). Under this scenario, local environment conditions select individuals with traits that provide them higher fitness ([Gaither2018](#)). At the population level, this results in populations adapting to their local environment, a mechanism coined "local adaptation" (Kawecki and Ebert, 2004) and resulting in patterns of "adaptive differentiation". Adaptive differentiation is hindered by dispersal, which prevents local adaptation by destabilizing the evolution of traits towards the optimal (Meszéna et al., 1997; Débarre et al., 2013; Mirrahimi and Gandon, 2020). While adaptive differentiation concerns traits under selection, it indirectly affects the differentiation of neutral traits, that are co-evolving with traits under selection through linkages (Billiard et al., 2015; Lepers et al., 2021). This results in turn to the mechanism of "isolation by adaptation", where habitat heterogeneity, rather than landscape connectivity, increases neutral differentiation ([nosil2008](#)). Simple mechanisms resulting in neutral and adaptive differentiation are identified, but how they are modulated by eco-evolutionary feedbacks and landscape complexity is unclear.

In ??, I demonstrate a novel mechanism, involving the process of intra-specific competition, that considerably affects neutral differentiation. Through the creation of unbalanced migration fluxes which increases the intensity of competition in highly connected populations, heterogeneity in connectivity reduces gene flow and reinforces neutral differentiation. I also investigate the mechanism of local adaptation in complex landscapes, where habitat connectivity is irregular. I show that the complexity of habitat spatial distribution can be reduced to a measure of habitat spatial auto-correlation, coined the "habitat assortativity". Landscapes characterised by a high habitat assortativity support populations that are systematically better adapted than in landscape with low assortativity. Specifically, I provide an analytical condition for local adaptation (??), that sheds light on how it relates to dispersal intensity, selection strength, habitat heterogeneity, and habitat assortativity.

Because habitat assortativity affects local adaptation, it must also affect neutral differentiation through the mechanism of isolation by adaptation. Closing the loop, I demonstrate that habitat assortativity affects neutral differentiation through two antagonistic effects. By favoring local adaptation, it promotes isolation by adaptation, therefore increasing neutral differentiation. In parallel, it also favors gene flow within clusters of similar environmental conditions, decreasing isolation by limited dispersal. This results in habitat assortativity decreasing neutral differentiation for low dispersal intensity, and increasing neutral differentiation for high dispersal intensity. This complex feedback is essential to understand population differentiation in complex landscapes. I provide a graphical summary of the feedback mechanisms shaping neutral and adaptive differentiation identified in ?? in Fig. 2.1. Overall, ?? establishes a complete map of causal pathways involved in the phenotypic differentiation of populations structured in complex landscapes.

## 2.1.2 Linking economic patterns to eco-evolutionary processes

By confronting fine-grained empirical data and process-based models, ?? bridges evolutionary economics, economic complexity and biology to better understand the endogenous drivers of economic development. Neoclassical economics and evolutionary economics



**Fig. 2.1:** Summary of the causal pathways involved in neutral and adaptive differentiation, disentangled in ???. Ecological processes are displayed in green boxes, evolutionary processes are displayed in red boxes.

seek to explain economic change with process-based models, focusing on the relationships between aggregated economic variables such as output, employment and productivity (Boschma and Frenken, 2005). In particular, evolutionary economics tries to understand economic change by relating it to endogenous forces, such as interactions between firms and economic activities, and evolutionary processes acting upon them (Metcalfe2006; Hodgson, 2019). In contrast, complexity economics uses fine-grained empirical data to investigate economic change (Hidalgo, 2021). Instead of process-based models, dimensionality reduction techniques are used to process the data and predict variations in national income (Mitchell, n.d.). While a current concern in evolutionary economics is to test the explanatory power of the proposed process-based models Hodgson, 2019, complexity economics seeks to unfold the causal processes underlying the success of the dimensionality reduction technique (Hidalgo, 2021).

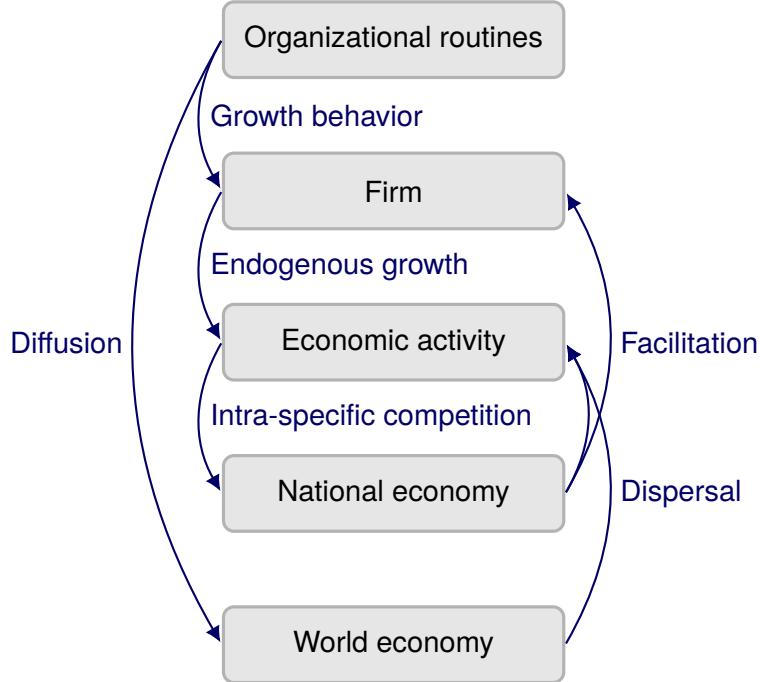
?? confronts process-based models and data to underpin the processes responsible for economic change. Our approach relies on deep connections between processes acting upon economic activities and biological populations. Analogously to biological populations that are characterized by genes, economic activities are characterised by organizational routines (NelsonWinter), which experience evolutionary processes and define how they engage in ecological processes (NelsonWinter). As a result, economic activities can be considered as autonomous entities, which dynamics is determined by its characteristics and the processes acting upon them (Boschma and Frenken, 2005). The temporal dynamics of economic activities contain signatures, i.e. distinctive temporal variations and couplings,

left by the most important processes at stage. Population dynamic models, combined with inverse modelling methods, can therefore be used to recover the role of the eco-evolutionary processes on the dynamics of economic systems, extracting this information from signatures in historical dynamics data.

Specifically, ?? explores the effect of processes involving positive and negative interactions between economic activities, spatial transfers, and economic activity transformations, on the dynamics of economic activities at the national scale. Using population dynamic models capturing the different interdependencies, ?? provides empirical evidence that economic activities engage in positive interactions, and benefit from spatial transfers of knowledge and routines. Positive interactions may arise from a variety of processes proposed in the evolutionary economic literature, such as supply chains (Ozman, 2009; Saavedra et al., 2009) and knowledge spillovers (Menon, 2015). Its support implies the dynamics of economic activities are highly inter-dependent, and suggest that diversity promotes economic development (**Hidalgo2018**). The support for spatial transfers implies that transfers of knowledge and organisational routines (Zahra et al., 2000; Zahra et al., 2000; Rogers, 2003; Boschma et al., 2008) have a considerable effect on economic activities. Nevertheless, discrepancies in the strength-of-evidence obtained for spatial transfers across countries highlight that some countries are overall more akin to spatial transfers than others, which may be explained by differences in cognitive, organizational, social, institutional or geographic proximities across countries (Boschma, 2005). I provide a graphical summary of the mechanisms evidenced in economic systems in ?? in Fig. 2.2. Overall, ?? evidences that, akin to biological systems, processes of interaction and dispersal shape the dynamics of economic systems at the country scale.

### 2.1.3 Advances in the modelling of realistic spatial and phenotypic structures

???? deliver new approaches to incorporate important features of empirical systems within eco-evolutionary models. Evolutionary dynamics have been traditionally studied in the context of regular population structures (Lieberman et al., 2005). For instance, to investigate differentiation in biological populations, Slatkin, 1973; Slatkin, 1978; Kirkpatrick and Barton, 1997; Polechová and Barton, 2015; Polechová, 2018; AndradeRestrepo et al., 2019; Doeblei and Dieckmann, 2003; Meszéna et al., 1997; Yeaman and Otto, 2011; Débarre et al., 2013; Mirrahimi and Gandon, 2020 consider regular spatial structures, missing the effect of spatial complexity on the underlying mechanisms. Biological habitats differ in their connectivity (Dale and Fortin, 2010), and economic entities are structured through complex networks (Schweitzer et al., 2009). Lieberman et al., 2005 and subsequent studies of "evolutionary dynamics on graphs" (e.g., Tkadlec et al., 2019) show that this complexity affects the interplay between selection and drift. However, evolutionary dynamics on graphs does not consider eco-evolutionary feedbacks (Govaert et al., 2019). Thus far, models that capture eco-evolutionary feedbacks together with realistic, complex population structures were missing.



**Fig. 2.2:** Summary of the eco-evolutionary processes evidenced in ??, and how they affect the different organizational levels in economic systems.

Another important feature of biological populations that may affect their dynamics is the variety of traits that characterize them (Doebeli2011). While a vast majority of the work on eco-evolutionary feedbacks has focused on the evolution of scalar phenotypes (Doebeli2011), in most organisms, many phenotypic properties combine in complicated ways to determine ecological processes (Doebeli2014). For instance, Doebeli2011 shows that the consideration of multiple traits is likely to generate more diversity than expected with one dimensional models. Trade-offs in traits is also an essential feature shaping the evolutionary dynamics of biological populations, with consequences on the dynamics of e.g. cancer cell evolution (Fiandaca2021) and plankton dynamics (Le Gland et al., 2020). Yet the simulation of eco-evolutionary models capturing the evolution of high dimensional phenotypic distributions is tremendously difficult, since the numerical cost of traditional methods grows exponentially in the number of dimensions of the phenotypic space (Bellman, 2010).

From first principles, ?? derives a stochastic individual-based model capturing eco-evolutionary feedbacks in populations structured in complex landscapes and high dimensional phenotypic space, and ?? provides tools to efficiently simulate a deterministic approximation of the model in high phenotypic dimensions. The individual-based model presented in ?? involves the combination of graphs and high dimensional phenotypic spaces, together with eco-evolutionary feedbacks, to model population structures. The model can readily be generalized to include other processes (see ?? for an extended variant with trait-based competition), and the Julia library **Evoid.jl**, written to run the numerical experiments in ??, already implements a generic version of the model. As such, the

model presented in ?? and the Julia library **Evoid.jl** may be used to investigate other questions involving complex population structures Lieberman et al., 2005 and the co-evolution of characteristics (**Doebeli2011**). Reproducing the discrete and stochastic nature of ecological and evolutionary processes (Champagnat et al., 2006), numerical simulations of individual-based model may not provide a general understanding of system investigated (**Lyon2016**), and cannot be scaled to simulate large systems involving millions of individuals DeAngelis and Mooij, 2005. Yet, the individual-based model proposed in ?? is mathematically tractable under simplifying assumptions, and can be efficiently simulated with a deterministic PDE approximation. Tractability allows to obtain analytical insights on how structural properties affect macroscopic population under simplifying assumptions (??). The PDE approximation, combined with the numerical methods presented in ??, further allow efficient simulations. The numerical methods proposed in ?? are now implemented in the Julia library **HighDimPDE.jl** (**HighDimPDE**), a registered Julia package belonging to the SciML organisation (**SciML**). The user interface respects standards from the SciML organisation, meaning that Julia users can easily adopt it. The package aims at hosting many more solver algorithms that break down the curse of dimensionality, and has, as of September 2022, already received contributions from 5 independent developers (see <https://github.com/SciML/HighDimPDE.jl/graphs/contributors>). These contributions may greatly enhance **HighDimPDE.jl** over the years, promising efficient simulations of eco-evolutionary models. Together, ??? deliver novel tools to advance our understanding on the effect of the complexity of population and phenotypic structures on eco-evolutionary dynamics in complex adaptive systems.

## 2.1.4 Advances in inverse modelling for identifying eco-evolutionary processes in empirical systems

Our understanding and prediction of eco-evolutionary dynamics in biological and economic systems critically depends on the confrontation of process-based models with empirical data (Pelletier et al., 2009; Hidalgo, 2021). The most celebrated inference methods for inverse modelling in biology are Bayesian inference methods with Markov Chain Monte Carlo (Lignell et al., 2013; Higgins et al., 2010; Xu et al., 2006; Fiechter et al., 2013; Rosenbaum et al., 2019) and variational methods (Schartau et al., 2017). Bayesian inference methods require numerous forward model integrations (Schneider et al., 2017), and are highly affected by the number of model parameters (Csilléry et al., 2010). Variational methods require the model sensitivity to its parameters (Schartau et al., 2017) and are prone to converge to local minima, especially with complex models (Gábor and Banga, 2015). Those central issues likely explain the very limited use of inverse modelling to further our knowledge on eco-evolutionary processes in biological systems (but see **Sukumaran2016**; **Skeels2019**; Skeels et al., 2022 that use approximate Bayesian computation methods).

?? presents a novel inverse modelling framework that allows to estimate the parameter values and the support of complex eco-evolutionary models from time-series data. The framework is based on a variational method, but resolves its main shortcomings by heavily relying on automatic differentiation (Rackauckas et al., 2020b), state-of-the-art optimizers

(Kingma and Ba, 2014), and a learning strategy based on a mini-batch method. The use of automatic differentiation simply eliminates the effort required to obtain the model sensitivity to its parameters, and the state-of-the-art optimizers, together with the mini-batch method, ensure the efficiency and reliability of the method in handling highly nonlinear models. ?? takes part in an ongoing effort to blend ML and traditional models to gain scientific understanding and extrapolability (Karpatne et al., 2017; Rackauckas et al., 2020b; Schneider et al., 2017; Rolnick et al., 2022; Kashinath et al., 2021; Yazdani et al., 2020; Raissi et al., 2019). In physical systems such as ocean and atmospheric systems, general organizational principles are known and formulated in general models. There, ML is mostly used to improve model forecast skill (Schneider et al., 2017). In contrast, general models of biological and economic systems are yet to be formulated, and methods such as the ML framework presented in ?? can greatly contribute to identify the general organizational principles required to reach this goal (Karpatne et al., 2017). By contrasting competing hypotheses embedded in alternative models, ???? provide concrete examples, both with synthetic and empirical data, that the inverse modelling framework in ?? can successfully elucidate eco-evolutionary mechanistic pathways. Integrating the practical constraints of current biological datasets (Dornelas et al., 2018), the inverse modelling framework may also be relevant for providing forecast ability to existing eco-evolutionary model (Norberg et al., 2012), and help to anticipate the response of ecosystems to climate change (Urban et al., 2016). Built thanks to the composability of the celebrated differential equation solver **DifferentialEquations.jl** and the deep learning library **Flux.jl**, the inverse modelling framework is implemented in the multi-purpose Julia package **MiniBatchInference.jl** (**MiniBatchInference**), readily available to the scientific community. Together, the inverse modelling framework proposed in ?? successfully blends ML methods with mechanistic ecosystem models to improve our gain scientific knowledge from observation data. Concrete case examples in ???? show that it enables the testing of eco-evolutionary theories against data, can potentially help to provide better forecasts of ecosystems states (Urban et al., 2016).

## 2.2 Limitations

### 2.2.1 Forward modelling

Alternative methods to those presented in ???? may be more appropriate for the forward modelling of eco-evolutionary dynamics. While individual-based models are interesting tools to investigate stochastic drift in finite size populations, the Gillespie algorithm (Gillespie, 1976) used to simulate the individual-based model in ?? is computationally intensive, and requires to compute the fitness of all individuals at each birth or death event, which depends on the characteristics of all the other individuals. The resulting computational complexity scales poorly with the number of individuals involved, preventing its use to model large populations. Individual-based models can be approximated by PDE models under simplifying assumptions (Champagnat et al., 2006), which are computationally more efficient in large populations for low dimensional phenotypic spaces ( $\lesssim$  3-dimensional). The methods presented in ?? can efficiently simulate PDE models in higher dimensions

(demonstrated up to 10 traits), but still suffer from a number of issues that may prevent their practical use. First, the MLP method can only provide the population number for one single trait value in one run. Consequently, the MLP method cannot characterize the total population density with a reasonable computational complexity. In contrast, the ML-based approximation method can provide the full population density, but involves the training of many neural networks (one at each time step). This is worrying, since the training of a neural network is numerically costly, and that long simulation times may be required by practitioners. Another problem with the numerical methods proposed in ?? is that they involve the tuning of meta parameters, including the choice of a measure for the integration of the non-local term ( $\nu_x$  in ???). This measure is critical for the success of the numerical simulations, but how to determine it is unclear. Together, the methods proposed in ?? may require further development to be used in practice by practitioners.

Because PDE models track the evolution of the full phenotypic density of populations, PDE models inevitably require a considerable computational effort - irrespective of the numerical method used. Nevertheless, only the first three moments of the population density are usually of interest, namely population size, trait mean and trait variance (Nordbotten et al., 2020). Instead of seeking to numerically approximate the full phenotypic density, moment closure approximation methods (Wickman2021; Lion et al., 2022; Nordbotten et al., 2020) may be considered. Those approaches consist in approximating the population density with a Gaussian distribution. This, in turn, allows to transform the PDE problem into a system of coupled differential equations involving the time evolution of the population size (1 variable for a single species population), the mean trait values ( $d$  scalar variables), and the variance-covariance matrix of the multidimensional trait density ( $d^2$  variables). As such, the computational cost of this method only scales polynomially with the number of dimension ( $\mathcal{O}(d^2)$ ), while providing the sufficient information required to investigate eco-evolutionary dynamics in high dimensional phenotypic spaces. It is worth noting that instead of using neural networks, Gaussian functions could also be used within the ML-based method for simulating eco-evolutionary models. Equivalent to the simplifying assumption taken with moment closure methods, we expect this approach to greatly improve the computational efficiency of the ML-based method, while solving the problem of the choice of a kernel for the integration of the nonlocal term. Using Gaussian functions may considerably lower the number of iterations required in the training process, while reducing the computational cost, as they involve fewer free parameters ( $d(d + 1) + 1$ ) than neural networks ( $xx$  in ??).

Together, the proposed methods in ??? suffer from considerable computational cost, because they seek to simulate PDE models which track the evolution of the full phenotypic distribution of populations. Because only the population number, the mean and the variance-covariance matrix of the phenotypic distributions are of interest, closure approximation methods could be considered. Those methods are compatible with the ML-based method proposed in ??.

## 2.2.2 Inverse modelling

The inverse modelling framework proposed in ?? and used in ?? also present pitfalls, which may favor the use of other methods to infer eco-evolutionary processes from empirical data.

First, the mini-batching learning strategy requires the choice of a minibatch size to ensure the convergence to the maximum likelihood estimate. This choice should be motivated by the roughness of the model likelihood landscape (see ??), but may affect the model selection process: a small batch size implies that the model goodness-of-fit is evaluated on the fast dynamics of the data, but the resulting support could differ, were the model fitted with a higher minibatch size. Theoretical developments are required to provide statistically justified guidance for the choice of this meta parameter. Second, the maximum likelihood estimate of models with complex likelihood landscape may be underestimated, because not correctly identified. As a result, the model selection process may be biased towards models with easier to navigate likelihood landscapes. Third, the information criterion-based model selection procedure used in ??? is uniquely based on a trade-off between the goodness-of-fit and the number of parameters of the model, which may not be satisfactory to characterize process-based model (Clermont and Zenker, 2015). Other criterion, involving the complexity of the dynamical behavior of the model (such as, e.g., its Lyapunov exponent), could be developed. Fourth, the inverse modelling framework developed in ?? requires a differentiable model, a strong prerequisite that may not be met by stochastic models. Fifth, the inverse modelling framework only provides the maximum of the posterior distribution, while the posterior distribution may be multimodal. The alternative modes may carry valuable information to consider in the model selection process (Daniels2015).

Alternatively, Sukumaran2016; Skeels2019; Skeels et al., 2022 employ variants of approximate Bayesian computation methods for eco-evolutionary model selection (Csilléry et al., 2010). The approach consists in aggregating model simulation outputs into summary statistics, used to train classifier algorithms (e.g., random forests or neural networks) in recognizing the signatures of the competing models. Once trained, the classifier algorithms are used on summary statistics obtained from the empirical data, discriminating between the alternative hypotheses. This approach does not require model differentiability, and is consequently more flexible than the method proposed in ?. Also, the use of summary statistics can elucidate which particular feature of the empirical data is better explained by a given model. Nevertheless, this strength is a pitfall: summary statistics necessarily reduce the information contained in empirical data, which can prevent to correctly discriminate between models (Csilléry et al., 2010). Together, the minibatch inverse modelling framework in ?? is sensitive to the minibatch size, requires models to be differentiable, and does not provide uncertainty estimation. While approximate Bayesian computation may be a valuable alternative, it also presents restrictive shortcomings. Still, the minibatch learning strategy extends beyond the framework proposed, and could be used in combination with novel approaches in Bayesian computation to combine the best of both worlds.

## 2.3 Perspectives

### 2.3.1 Development opportunities in inverse modelling

The mini-batch method presented in ?? and the ML-based approximation method developed in ?? offer unique development opportunities to leverage inverse modelling. The mini-batch

method is relevant beyond the ML framework presented in ??, and could be used within a fully Bayesian framework, where the full posterior distribution of the model is estimated. Compared to considering a plain vanilla likelihood function such as ?? for Bayesian inference, the minibatch loglikelihood formulation proposed in ?? would result in a smoother posterior distribution, potentially reducing the number of forward model integration. While this number could still be prohibitively expensive for Bayesian inference with MCMC chains (see ??), automatic differentiation variational inference (ADVI, **Morningstar2020**; Gosh et al., 2021) offers an appealing alternative. In ADVI, the posterior distribution is approximated by a Gaussian distribution (**Morningstar2020**), significantly reducing the number of model integration (**Morningstar2020**). Improving the ML framework presented in ??, ADVI could capture multimodality in the model posterior distribution (by approximating the multimodal distribution with a gaussian distribution with large variance). This, in turn, could improve the robustness of model selection (??), and provide uncertainties estimations on the parameters. Bayesian Learning via Stochastic Gradient Langevin Dynamics (**Welling2011BayesianIV**) is an alternate solution to ADVI, that could readily be used with the ML framework proposed in ?? instead of the optimization algorithms suggested. This algorithm builds upon recent advances in Bayesian Deep Learning (**Wilson2020**), and interprets the iterative gradient-based optimization procedure as a Markov chain with an equilibrium distribution over the posterior distribution of the model parameters. It therefore comes with the scalability of variational methods and the interpretability of Bayesian methods, providing uncertainty estimates while ensuring computational efficiency.

For inverse modelling with PDE models, an extension of the ML-based approximation method presented in ?? could yield interesting performance. In ??, the parameters of the PDE model are assumed fixed, but could be set as free parameters, analogously to the parameters of the neural networks used for approximating the solution. The loss function in ?? would then take the PDE model parameters as additional arguments, and include an additional term, penalizing the distance between the PDE model solution and the data. This term, analogous to ?? in ??, would constrain the PDE parameters, similarly to the training of physics informed neural networks (Raissi et al., 2019; Yazdani et al., 2020). Yet in contrast to Raissi et al., 2019; Yazdani et al., 2020, a major advantage of this approach it to efficiently perform inverse modelling with high-dimensional dynamical models. Because Julia is a programming language with pervasive AD (see ??), this development would require little effort with the Julia library **HighDimPDE.jl**. Together, the ML methods developed in ???? offer unique opportunities to bring more robustness and efficiency to inverse modelling methods, providing uncertainty estimation and the possibility to handle high dimensional models.

### 2.3.2 Confronting eco-evolutionary model on spatial graphs and empirical data

The confrontation of the predictions demonstrated in ?? with empirical data, and the use of empirical data to constrain the eco-evolutionary model on spatial graphs, could advance our understanding of eco-evolutionary dynamics in empirical systems. In ??, we predicted three

topology metrics to correlate with standard population differentiation metrics ( $Q_{ST}$  metrics). By projecting real landscapes on spatial graphs (see Dale and Fortin, 2010 and ??), the topology metrics, together with empirical data on population differentiation (e.g., (Manel et al., 2003)), could be used to verify our predictions. Discrepancies may indicate that additional processes are involved in population differentiation in empirical systems. On the other hand, a validation of our predictions could help to predict population differentiation at a global scale. These predictions could, in turn, be linked to patterns of species richness, in order to underpin how population genetics may lead to speciation over time (Templeton, 1981). As regards to explaining spatial biodiversity patterns, simulations of the eco-evolutionary model on spatial graphs over geological time, using paleo-climatic data (**STRAUME2020126**) as environmental condition forcings within, could help to address fundamental questions on the processes involved. In contrast to deep-time spatially explicit eco-evolutionary models (see Hagen, 2022 for a review), the model developed in ?? accounts does not assume a time scale separation between ecological and evolutionary processes. This would allow disentangling, for instance, the role of feedbacks between trait-based competition (Dieckmann and Doebeli, 1999) - succinctly considered in ?? (see ??) -, and environmental filtering (Doebeli and Dieckmann, 2003), in shaping patterns of species distribution in empirical landscapes Rahbek et al., 2019a. Along shorter time scales, the eco-evolutionary model on spatial graph could be calibrated on empirical data of species distribution **Abegg2020; Gisler2008; GBIF:TheGlobalBiodiversityInformationFacility2022** with the inverse modelling method proposed in ??, and combined with climate scenarios (**Kriticos2012**) to better predict how biological populations will adapt to climate change (Norberg et al., 2012; Urban et al., 2016). Together, the model developed in ?? and the resulting predictions, together with the ML framework presented in ??, could bring insights on the actual mechanisms involved in empirical systems, and help to predict their responses to climate change.

### 2.3.3 Econobiology, a new venue to understand economic systems, and design more appropriate governance

The success of the biologically inspired model presented in ?? in characterizing the dynamics of aggregate economic activities calls for a deeper investigation of commonalities and differences in organizational principles in biological and economic systems. As a first step, I suggest investigating whether the results of ?? hold for finer levels of economic activity aggregation, as more detailed data on economic activities is available (Hausmann and Hidalgo, 2011). Second, the eco-evolutionary models should be complexified, to investigate whether it can capture more detailed aspects of the dynamics. In parallel, an essential research direction is to better understand how capital fluxes (**King1993**) compare with fluxes of matter and energy (Veldhuis et al., 2018) in ecological systems. Veldhuis et al., 2018 provides a synthesis of our understanding of how ecosystem organization emerges through self-reinforcing mechanisms, promoted by ecological and evolutionary processes acting upon fundamental ecological compartments such as producers, consumers, and decomposers. This synthesis is an interesting roadmap to formulate hypotheses and investigate analogous self-reinforcing mechanisms determining fluxes of capital in economic

systems. There may be deep connections between nutrient cycles and capital cycles, where ecological compartments and financial intermediaries develop to improve the efficiency of nutrient flows and capital allocations (Odum, 1969). King1993; Veldhuis et al., 2018 show that, in both ecological and economic systems, this efficiency sustains productivity and growth, but that the developmental process may fail. In the latter case, ecosystems may stay in a state of lower maturity (Margalef1963) and economies may be stuck in a technological lock-in (Hidalgo2009). I expect that this research venue will eventually pinpoint at key organizational differences between ecological and economic systems. Since ecosystems have undergone evolution for a much longer time than economic systems, they may be more effective and resilient than economic systems, providing models for economic policies. Together, future directions should seek to understand similarities and differences in organizational principles in ecological and economic systems, which may eventually provide guidance for improving economic regulations.

## 2.4 Concluding remarks

Bridging biology, mathematical modelling, machine learning and economics, this thesis advances our general understanding of eco-evolutionary processes and feedbacks in biological and economic systems. While we now better understand eco-evolutionary feedbacks in spatially structured populations, we are far from understanding how different population . A general understanding of biological systems may and presents novel methods to further improve this knowledge.

general organizational principles in biological and economic systems.

contributed to a better understanding of eco-evolutionary dynamics in biological and economic systems. We are far from a

To conclude, this thesis presents novel forward and inverse modelling methods to better understand the dynamics of structured populations, and to use them in combination with empirical data to infer knowledge. These methods allow to establish a map of causal pathways involved in local adaptation and phenotypic differentiation of spatially structured biological populations, and highlights that processes akin to those in biological systems shape the dynamics of economic systems. In the face of the climate and biodiversity crisis ahead of us, it is of utmost urgency to quickly advance our general understanding of the mechanisms shaping our world. Bridging biology, mathematical modelling, machine learning and economics can massively accelerate this understanding. It is, more than ever before, urgent to better understand and forecast the dynamics of life on Earth. While we know that the global temperature on Earth will rise by 2 to 4 degrees in 2100, predictions on ecosystem states are much more uncertain. Yet obtaining more realistic ecosystem forecasts is critical to help designing adequate management of ecosystem services. Blending scientific knowledge, formalised in mathematical model, with machine learning, provides unique opportunities to quickly improve our understanding of ecosystem dynamics and provide forecasts. Machine learning is part of the astonishing technological progress experienced by humankind in the last centuries. This progress has led us to think that we are rational beings, that have crafted singular socio-economic to create wealth. Yet it may well be that

socio-economic systems are analogous to, but less efficient and resilient than, biological systems. Realising overlaps and differences in processes shaping economic and biological systems may be extremely beneficial: we could surely take inspiration from organizational principles in biological systems, that have survived major environmental crisis for more than 3.5 billion years. To conclude, let me cite Hölderlin: "*To be but one with all living things, to return, by a radiant self-forgetfulness, to the All of Nature*".



# CV

## Personal Information

<b>Residence</b>	Zürich, Switzerland
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<b>Github</b>	github.com/vboussange
<b>Age</b>	Born 1995 (age 27)
<b>Citizenship</b>	France citizen

## Personal skills

<b>Languages</b>	English (fluent) French (native) Spanish (B2) German (B1)
<b>Programming languages</b>	Julia Python C++ Java Matlab R Bash VBA
<b>Sports</b>	Ski mountaineering Alpinism Rock climbing Enduro mountainbiking Surfing
<b>Alpine CV</b>	[ <a href="http://vboussange.github.io/pages/alpine_cv/">vboussange.github.io/pages/alpine_cv/</a> ]

## Education

- 10.2022 **Ph.D in Environmental Sciences**, Swiss Federal Institute for Forest, Snow and Landscape (WSL | Swiss Federal Institute of Technology Zurich, ETH), Switzerland  
 09.2018 *Forward and inverse modelling of eco-evolutionary processes in biological and economic systems.* Under the guidance of Prof. Dr. Loïc Pellissier.

- 06.2017 **Full year academic exchange**, University of New South Wales (UNSW Sydney),  
09.2016 Australia
- 06.2017 **Master thesis in theoretical geomechanics**, UNSW Sydney | CSIRO, Australia  
02.2017  
*Numerical continuation and bifurcation analysis for unconventional geomechanics.*  
Under the guidance of Dr. Thomas Poulet.
- 08.2018 **M.S. in Energy and Environmental Engineering**, Institut National Des Sciences Appliquées de Lyon (INSA Lyon), France  
09.2013 Three-year undergraduate engineering course in Energy and Environmental Systems, focused on Advanced Energy Systems and Efficiency.
- 08.2018 **B.S. in Mathematics and Physics**, Institut National Des Sciences Appliquées de Lyon (INSA Lyon), France  
09.2013 Ranking : 21/650 students.

## Professional appointments

- 08.2018 **R&D intern**, Compagnie National du Rhône (CNR), France  
03.2018 Development of an Energy Management System based on various optimisation techniques for optimal production of renewable resources. Applications to EU sponsored projects: **Jupiter1000** (power-to-gas), **Move in pure** (vehicle-to-grid), **Marie-Galante island** (micro-grid)

## Publications

### Peer-reviewed

1. **Boussange, V.** & Pellissier, L., *Eco-evolutionary model on spatial graphs reveals how habitat structure affects phenotypic differentiation.* **Commun Biol** 5, 668 (2022). [[bioRxiv](#)]

### Preprints

1. **Boussange, V.**, Vilimelis-Aceituno, P., Pellissier, L., *Mini-batching ecological data to improve ecosystem models with machine learning* [[bioRxiv](#)] (2022), 46 pages. In review.
2. **Boussange, V.**, Becker, S., Jentzen, A., Kuckuck, B., Pellissier, L., *Deep learning approximations for non-local nonlinear PDEs with Neumann boundary conditions.* [[arXiv](#)]

(2022), 59 pages. Revision requested from Partial Differential Equations and Applications.

## Proceedings

1. Poulet, T., Alevizos, S., Veveakis, M., **Boussange, V.**, Regenauer-Lieb, K., *Episodic mineralising fluid injection through chemical shear zones*, ASEG Extended Abstracts (2018), 5 pages.

## In preparation

1. **Boussange, V.**, Sornette, D., Lischke, H., Pellissier, L., *Analogous forces to ecological interactions, dispersal and mutations shape the dynamics of economic activities*.

## Talks

- 07.2022 **Speaker**, HIGHDIMPDE.JL: A Julia package for solving high-dimensional PDEs, JuliaCon2022, online. [youtube.com/watch?v=4sXqGhhknT4](https://youtube.com/watch?v=4sXqGhhknT4)
- 06.2022 **Speaker**, Interpretable machine learning for forecasting dynamical processes in ecosystems, World Biodiversity Forum, Davos, Switzerland.
- 06.2022 **Invited speaker**, Investigating empirical patterns of biodiversity with mechanistic eco-evolutionary models, Seminar at the Theoretical Ecology and Evolution group, Universität Bern.
- 11.2021 **Invited speaker**, Numerical approximations of solutions of highly dimensional, non-local nonlinear PDEs, StAMBio seminar, St Andrews, UK.
- 10.2021 **Speaker**, Graph topology and habitat assortativity drive phenotypic differentiation in an eco-evolutionary model, Conference on Complex Systems, Lyon, France.
- 10.2021 **Speaker**, Using graph-based metrics to assess the effect of landscape topography on diversification, ECBC, Amsterdam, Netherlands.
- 09.2021 **Speaker**, Solving non-local nonlinear Partial Differential Equations in high dimensions with HighDimPDE.jl, International Conference on Computational Methods in Systems Biology, Bordeaux, France.
- 04.2021 **Speaker**, Responses of neutral and adaptive diversity to complex geographic population structure, Mathematical Population Dynamics, Ecology and Evolution, CIRM Marseille, France.

## Softwares

- 2022 **MiniBatchInference.jl** Julia  
[github.com/vboussange/MiniBatchInference.jl](https://github.com/vboussange/MiniBatchInference.jl)  
A Julia package for maximum likelihood estimation and model selection of strongly nonlinear dynamical models.

2021	<b>HighDimPDE.jl</b> <a href="https://github.com/vboussange/HighDimPDE.jl">github.com/vboussange/HighDimPDE.jl</a>	Julia
A Julia package that breaks down the curse of dimensionality in solving non local, non linear PDEs.		
2021	<b>EvoId.jl</b>	Julia
2019	<a href="https://github.com/vboussange/EvoId.jl">github.com/vboussange/EvoId.jl</a>	
	Evolutionary individual based modelling, mathematically grounded.	
2018	<b>OptiVPP</b> <a href="#">confidential</a>	Python, GAMS
	Energy Management System for Virtual Power Plants.	

## Open source software contributions

SciML  
 DiffEqFlux.jl  
 CUDA.jl  
 Flux.jl  
 LightGraphs.jl

## Teaching and supervision

12.2020	<b>701-3001-00L Environmental Systems Data Science</b> , ETH Zürich, D-USYS,
09.2020	Switzerland
06.2020	<b>262-0100-00L Lab rotation</b> , ETH Zürich, D-BSSE, Switzerland
04.2020	
12.2020	<b>Taste of research internship</b> , Polytech Nice-Sophia, France
09.2020	

## Reviews

2022	<b>Journal of Open Source Software</b>
2019	<b>Journal of Theoretical Biology</b>

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