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IDEA AND PERSPECTIVE

To what extent can ecosystem services motivate protecting biodiversity?

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Abstract

Society increasingly focuses on managing nature for the services it provides people rather than for the existence of particular species. How much biodiversity protection would result from this modified focus? Although biodiversity contributes to ecosystem services, the details of which species are critical, and whether they will go functionally extinct in the future, are fraught with uncertainty. Explicitly considering this uncertainty, we develop an analytical framework to determine how much biodiversity protection would arise solely from optimising net value from an ecosystem service. Using stochastic dynamic programming, we find that protecting a threshold number of species is optimal, and uncertainty surrounding how biodiversity produces services makes it optimal to protect more species than are presumed critical. We define conditions under which the economically optimal protection strategy is to protect all species, no species, and cases in between. We show how the optimal number of species to protect depends upon different relationships between species and services, including considering multiple services. Our analysis provides simple criteria to evaluate when managing for particular ecosystem services could warrant protecting all species, given uncertainty. Evaluating this criterion with empirical estimates from different ecosystems suggests that optimising some services will be more likely to protect most species than others.

Keywords

Biodiversity conservation, biodiversity-ecosystem services, conservation decisions, ecosystem services, stochastic optimal control, uncertainty.

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INTRODUCTION

Many conservation organisations have shifted their stated objectives from preserving biodiversity to protecting nature for the benefits it provides to society – known as ecosystem services (Daily 1997; Balvanera *et al.* 2001; Polasky *et al.* 2005; Tallis *et al.* 2008; Turner & Daily 2008; Kinzig *et al.* 2011; Kareiva *et al.* 2014; Mace 2014). This expanded attention on nature's benefits to humans has spurred debates about its consequences for biodiversity protection (e.g., McCauley 2006; Kareiva & Marvier 2012; Doak *et al.* 2014). Proponents of ecosystem services argue that this broadened focus better aligns the interests of people and biodiversity conservation (Armsworth *et al.* 2007; Turner & Daily 2008), because service values can be large (Daily & Ellison 2002; Bateman *et al.* 2013) and biodiversity plays a key role in producing them (Balvanera *et al.* 2006, 2014; Díaz *et al.* 2006; Kinzig *et al.* 2011; Cardinale *et al.* 2012; Ricketts *et al.* 2016). This logic suggests that protecting some biodiversity is crucial to maintaining ecosystem services, and biodiversity's benefits extend beyond its existence value (Daily & Ellison 2002). Still, managing for services and protecting biodiversity are not identical goals; therefore, managing for some services may leave many species unprotected (Balvanera *et al.* 2001; Ghazoul 2007; Kremen *et al.* 2008; Venter *et al.* 2009; Polasky *et al.* 2012). In response, we ask: if conservation decisions were based solely on optimising the net value of ecosystem services, how much protection of biodiversity would arise?

Determining when managing for particular ecosystem services will result in protecting most species requires carefully considering two factors. First, only a subset of biodiversity provides any single ecosystem service, which might imply that protecting relatively few species could secure single services (Kleijn *et al.* 2015; Ricketts *et al.* 2016). Second, our understanding of the link between biodiversity and services is riddled with uncertainty (Balvanera *et al.* 2014). For instance, how results from small-scale studies that measure ecosystem function (e.g., biomass production) translate to large-scale ecosystem services is unclear (e.g., marketable crop production or reduced costs of fertilisers or pesticides) (Schwartz *et al.* 2000; Kremen 2005; Srivastava & Vellend 2005; Jiang *et al.* 2009). Similarly, the details of how most species, functional traits, and genotypes contribute to services are typically poorly understood (Polasky *et al.* 1993; Loreau *et al.* 2001;

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Kremen 2005), especially under global change scenarios (Díaz *et al.* 2006). Uncertainty over which species provide services and whether they will go functionally extinct creates challenges for decision-makers tasked with managing biodiversity to secure ecosystem services. Indeed, uncertainty can influence optimal management decisions. On the one hand, this uncertainty could drive a precautionary approach, to maintain biodiversity to have the option to benefit from it in the future (Arrow & Fisher 1974; Traeger 2014). On the other hand, uncertainty can promote more aggressive exploitation of species and natural resources since there is a risk that those resources might be lost in the future (Costello & Grainger 2015). Given this tension, we need a formal way to understand how uncertainty affects the optimal level of species protection when managing for ecosystem services.

Here, we develop theory to determine when decision-makers seeking to secure ecosystem services would invest in species protection given uncertainty surrounding links between biodiversity and ecosystem services. This theory can apply to a broad range of services, including biodiversity itself (Millennium Ecosystem Assessment 2005; Mace *et al.* 2012), or services in which biodiversity acts as an input (e.g., to the value of carbon storage, crop pollination, or recreation). However, our analysis is limited to services for which the decision-maker is willing to quantify the value in monetary terms so that the net value of the service (its benefit minus the cost to secure it) can be evaluated.

Using this analytical framework, we address several interrelated questions: Does uncertainty about which species are critical to services reduce motivation for preservation (e.g., because many species may play no significant role) or increase motivation for preservation (e.g., because potential losses in service value could be far greater than the cost of protecting species that unknowingly play no functional role)? How many species are critical to protect to ensure the greatest expected net value of services? How does the number of species providing a service affect the economically optimal amount of biodiversity protection for ecosystem services? And, does considering multiple services raise the number of species that is optimal to protect, for instance, because different species might be needed for different services? We identify conditions under which ecosystem services would motivate protecting no species, a fraction of species, or – in rare cases – all species in an ecosystem. We also determine how the optimal number of species to protect scales with the number of species that deliver a service, the costs associated with species protection, more than one service, and the relationship between the number of species critical to a service and the service's value. This analytical framework and the criteria it yields help identify cases where managing for a specific set of ecosystem services would result in protection of most species, and when it would not.

A theory to quantify the value of ecosystem service objectives for biodiversity

We seek to determine the level of biodiversity protection that provides the highest net value of ecosystem services (measured in \$) over time in the face of uncertainty over which species need protection to secure services. We formulate a modelling framework informed by current knowledge about how biodiversity contributes to ecosystem services (Cardinale *et al.* 2012; Balvanera *et al.* 2014, 2016; Ricketts *et al.* 2016) using tools from economics and optimal control theory. Here biodiversity refers to species diversity, but the framework could also apply to functional groups. Our framework can consider any service that can be valued – with either market or non-market valuation – including provisioning, regulating, and some cultural services (Fisher *et al.* 2009; de Groot *et al.* 2010; Costanza *et al.* 2014). However, some services may not be appropriate to value in monetary terms, such as cultural services with spiritual, intrinsic, or relational value (Chan *et al.* 2016). We recognise that the ecosystem services framework includes these values (Díaz *et al.* 2015) but do not consider them in this analysis. For the types of services we can include, we do not judge what values or valuation process should be used.

Our theoretical framework builds on, yet differs from, existing approaches from both ecology and economics. One prominent previous approach compares spatial overlap in land management priorities when optimising ecosystem services and biodiversity as two distinct and independent objectives (i.e., assuming ecosystem services do not depend on biodiversity, Nelson *et al.* 2008; Polasky *et al.* 2008, 2012). A related literature explores tradeoffs between biodiversity and development objectives, where benefits from development do not depend on biodiversity persisting (e.g., Leroux *et al.* 2009). Further, most ecosystem service production models treat the environment either as a single input into the production of services (McConnell & Bockstael 2005) or in terms of proxies such as habitat area or type (Barbier 2007, 2013; Tallis & Polasky 2009; de Groot *et al.* 2010; Bennett 2016; *but see* Isbell *et al.* 2015). Alternatively, other studies consider how to best manage biodiversity in the face of uncertainty for its existence or bioprospecting value (e.g., the Noah's Ark problem, selecting which species to conserve to maximise the total differences among species, Weitzman 1998; Polasky *et al.* 2005) – but do not consider the role of biodiversity as an input into other ecosystem services in these decisions (e.g., its functional value, Mace *et al.* 2012). Finally, in those ecological studies that do address the functional relationship between biodiversity and ecosystem services, most do not explicitly consider decision-making for managing ecosystem services, dynamics, or the costs of species protection (e.g., Gamfeldt *et al.* 2013; Isbell *et al.* 2015; Winfree *et al.* 2015).

Our approach builds on this literature by considering a situation in which net ecosystem service value is the sole management objective, and the production of that value depends on biodiversity in an uncertain way. We model cases where the current and future values from ecosystem services depend on the presence or number of critical species persisting in the species pool, motivated by empirical findings (Balvanera *et al.* 2006, 2014; Cardinale *et al.* 2012). We also consider uncertainty over which species need protection to secure ecosystem services into the future. Given links between species and services – and uncertainty in this relationship – we derive the optimal strategy for investing in protecting species or not given the goal to maximise net service value over time.

Therefore, our modelling framework draws on results from ecology, while also explicitly considering a management objective of ecosystem services, decisions about species protection in the face of uncertainty, and the costs associated with those decisions.

We consider communities with two broad types of species: those critical to providing an ecosystem service (either directly or indirectly and obligately) and those that do not contribute to the service (Fig. 1). In real-world management scenarios, it is unlikely that we ever know all the species that are critical to a service, especially through time. For example, changes in climate and biogeochemical cycles alter which plant species contribute most to grassland ecosystem services (Isbell *et al.* 2011). Thus, managers face an inherent challenge of incomplete information. There is also uncertainty over which species will go functionally extinct (i.e., fall below the abundance at which they contribute measurably to a service) without active protection. In disturbed habitats, species face some perpetual threat of functional extinctions, such as from habitat loss, disease, overexploitation, and climate change (Tilman *et al.* 1994; Pereira *et al.* 2010). Our model accounts for both incomplete information over which species provide services and uncertainty over which species will be functionally lost (modeled as random losses).

Managing for ecosystem services presents the fundamental challenge of balancing the current costs of species protection against the future risks of losing ecosystem services. If managers do not know which species are critical for an ecosystem service, then each species that is functionally lost increases the risk that an ecosystem service will be lost or reduced. When a species is threatened by functional extinction, the management decision is whether or not to engage in costly protection of the species. Protecting species helps ensure that an ecosystem service is provided but necessarily incurs direct and indirect costs (Naidoo *et al.* 2006). We consider cost to have two components: the direct cost of protection and the opportunity cost of values forgone from activities that must be banned or reduced to protect species (e.g., harvesting species, developing land, Naidoo *et al.* 2006). Alternatively, not protecting does not incur a direct financial cost, but inaction risks the loss of a critical species, and therefore, costs associated with the loss of an ecosystem service (e.g., loss of crop productivity or water retention requiring increased irrigation). We quantify how much biodiversity protection best balances the current costs of protection with the current and future net service value, given uncertainty over the links between species and services.

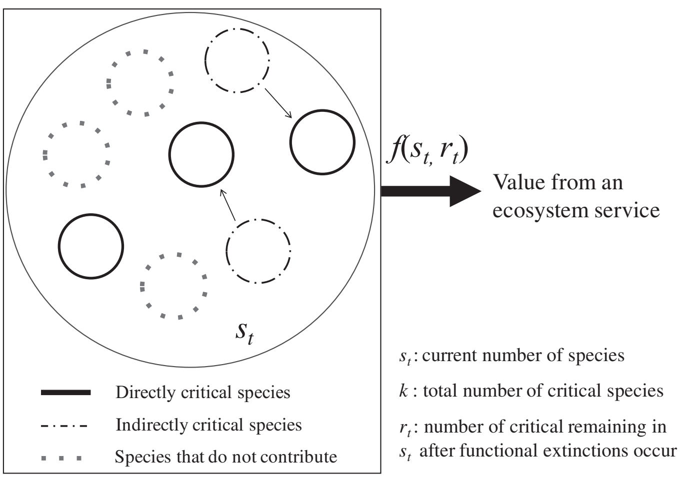

Figure 1 A conceptual diagram of how ecological communities produce services in our model. A subset of species is critical to a service either directly (e.g., pollinators) or indirectly (e.g., obligate prey of species targeted by fisheries). When the critical species persist in the species pool (of s_t species), an ecosystem service generates value for people. For most services, considerable uncertainty remains over how species pools map to value from ecosystem services.

METHODS

In our model, the objective is to maximise the expected net present value of ecosystem services over an infinite time horizon given uncertainty over the relationship between species and ecosystem service value (Fig. 1). Net present value is the expected net value from a service less any costs of protection, summed and discounted over an infinite time horizon. We formulate the decision process as a stochastic optimal control problem (also known as a Markov Decision Process) and solve it using stochastic dynamic programing (SDP) techniques (Bellman 1954; see Marescot *et al.* 2013; De Lara & Doyen 2008 for primers). SDP determines a management strategy (called the optimal policy) that best achieves the decision-maker's objective over time. Here, the optimal policy generates the sequence of actions – investment in protection or not at each species pool size – that maximises the expected net ecosystem service value over an infinite time horizon.

Specifically, we consider a decision-maker managing a pool of species, among which some are critical to provide an ecosystem service (Fig. 1). We assume the number of critical species is known, but their identities are not known. Therefore, the manager has imperfect information about which species are critical to the service. During each time period, one species will go functionally extinct, except if costly protection measures are taken. Species losses occur randomly. Together, this creates uncertainty over whether the species that will be functionally lost without protection will be one critical to the service. We formulate this problem with the following setup and variables.

(1) *State variables*: At the beginning of every period, the decision-maker observes the size of the current species pool (s_t), in number of species, and knows whether or not the service was obtained in the prior period. The ecosystem begins with s_0 species, of which k are critical to the service. The decision-maker knows the size of the subset k but not the identities of species in k. At any later time t, s_t denotes the remaining number of species, and r_t denotes the number of critical species that remain after some are functionally lost, with $r_t \in \{0, \ldots, k\}$.

(2) *Actions*: The manager chooses whether to protect or not protect the current species pool, s_t, after observing whether or not the service was obtained in the prior period. $d_t \in \{P, NP\}$ denotes this decision.

(3) *Dynamics*: When the manager does not protect the species pool, a random species will be lost in the next period. This action risks the loss of a critical species (from the subset k), and thus the reduction or full loss of the ecosystem service in the future.

(4) *Uncertainty*: When deciding whether to protect or not protect, the manager knows whether the service is currently being provided, but does not know which species are providing that service or which species will be lost if she does not protect. Thus, she is making a conservation decision under uncertainty about its future consequences.

(5) *Immediate payoffs*: The current period payoff from an ecosystem service depends on whether the service is provided and what action is taken. Investing in protection incurs a cost c, whereas not protecting incurs no cost. The immediate payoff is the difference between the benefits from an ecosystem service and these costs. We consider several functional relationships representing how the current period payoff from an ecosystem service, $f(s_t, r_t)$, depends on the number of critical species providing it (r_t). First, we analytically solve an extreme case that bounds our solution where all k critical species are required to provide the service (i.e., $r_t = k$): if $r_t = k$ then the service is provided, and a benefit of v is obtained; if not, the benefit is 0, meaning $f(s_t, r_t) \in \{0, v\}$. Then, we numerically solve for cases that more closely mimic empirical studies of ecosystem functions, where the level of service provision is an increasing function of the number of critical species. For these cases, the payoff function is $f(s_t, r_t) = v(r_t)$, which we denote $v_{r,}$ where r_t is the number of remaining species in the community that contribute to the service and is $\leq k$ (see Supporting Information 1). We consider several forms of v_r, including linear (Gamfeldt *et al.* 2015), convex/accelerating (Mora *et al.* 2014), or concave/saturating relationships (Cardinale *et al.* 2011; Reich *et al.* 2012; O'Connor *et al.* 2017).

(6) *Intertemporal value*: Optimising the net value of the ecosystem service over time means maximising the difference between service benefits (measured in dollars as revenues) and the costs incurred by protection. Future costs and revenues are discounted by a factor δ according to standard cost-benefit analysis techniques from economics (Arrow *et al.* 2013). The discount factor, δ, represents how the decision-maker weights the future relative to the present; for instance, $\delta = 0$ implies a preference to obtain value only in the present, while the present and future are weighted equally when $\delta = 1$.

To make this problem tractable, we assume that (1) the immediate service value is known and quantifiable (in \$) at each level of diversity, (2) species losses are random and do not lead to secondary extinctions (Solé & Montoya 2001; Allesina *et al.* 2009), (3) when species protection is chosen, it is successful but incurs a cost, c, which includes direct costs of protection and opportunity costs, and (4) when the service is lost, this loss is irreversible (i.e., no option for restoration). We restrict the decision-maker's actions at any time to *protect* or *not protect*. The assumption that protection costs are independent of the number of species protected is reasonable for several common types of protective actions (e.g., habitat protection that benefits all species or targeted protection activities that only focus on the species most threatened with functional extinction) but not all (e.g., invasive species control, restoration).

Based on this problem formulation, investing in species protection results in an immediate payoff of $f(s_t, r_t) - c$ (which is $v - c$ for the piecewise form and $v_r - c$ for the smooth relationships) plus a stream of expected future payoffs discounted by δ. When the species pool is not protected, the potential loss of service value through biodiversity loss must be considered, because a species critical for a service could be lost. The probability that the loss of a random species does not affect the service is $p(s_t, r_t) := \frac{s_t - r_t}{s_t}$ and depends on the size of the current species pool and the number of critical species remaining in it. If the species pool is large and the number of critical species is very small, the random loss of a species is unlikely to result in the loss of service value. When the decision-maker chooses not to protect, the resulting payoff may be either v_r with probability $p(s_t, r_t)$ or v_{r-1} with the probability $1-p(s_t, r_t)$. For the piecewise case, payoffs will be either v with probability $p(s_t) = p(s_t, k)$ or 0 (if a critical species is lost) with the probability $1-p(s_t)$. For a given period, the decision-maker will protect if the net payoff from protecting exceeds the expected value of not protecting. Analyses use expected payoffs and assume the decision-maker is risk neutral. Specifically, we find the optimal policy that solves the Bellman equation. For the piecewise case, this takes the form:

$$J(s_t) = \max_{d_t \in \{P, NP\}} \{v - c + \delta J(s_t), p(s_t)[v + \delta J(s_t - 1)]\}. \quad (1)$$

for $s_t \in \{1, \ldots, s_0\}$. The value from protecting is to the left of the comma, and the expected value from not protecting is to the right of the comma. We then extend this basic setup to consider different biodiversity-ecosystem service relationships [i.e., modifying the form of the immediate payoff and $p(s_t)$] and multiple services, as described below and in the Supplemental Information (Supporting Information 1).

Analytical approach

First, we solve the model analytically for the case where the functional loss of any one critical species causes complete and irreversible loss of the ecosystem service (i.e., the Bellman equation in eqn 1), using Theorem 1 and Proposition 3. Figure 2 illustrates the Theorem's logic (see Supporting Information 1 for proofs), which is as follows. Protecting the species pool of size s_t is optimal when current and future value from protecting (i.e., remaining in the state s_t) exceeds the expected value of not protecting (transitioning to $s_t - 1$). We find the s_t at which the optimal management strategy switches from not protecting to protecting based on the following. The value from protecting depends on $v - c$ and δ, but not on s_t. In contrast, the expected value of not protecting biodiversity grows with s_t, because the risk of losing the service from a random species loss decreases with s_t. When s_t is large, the value of not protecting can surpass the value of protecting. Because the difference between these two functions increases with s_t, they will cross at a unique value of s_t, bounded by 0 and $+\infty$ (Fig. 2). Above this unique value of s_t, denoted $\bar{s}$, *not* protecting is optimal; for species pools smaller than $\bar{s}$,

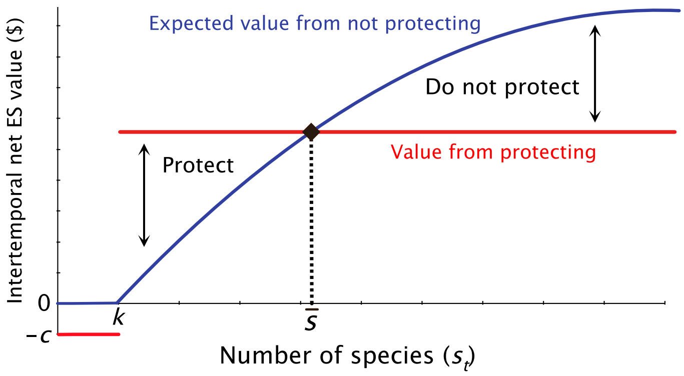

Figure 2 An illustration of the intuition behind the mathematical proof that finds the optimal number of species to protect, i.e. the analytical solution presented in eqn 3 that solves eqn 1. It compares the intertemporal net value of a service, as a function of the number of species (s_t), that results from protecting vs. the expected value from not protecting the species pool (conditional on retaining the service after species are functionally lost). k represents the number of species that are critical to the service. In the model we solve analytically given in eqn 1, all k species need to be in the species pool to obtain the service; thus, for both strategies (protect or not protect) when $s_t < k$, the service value is 0. For $s_t < k$, not protecting is therefore the optimal strategy. The expected value of not protecting increases with s_t, because the probability of losing the service from a random extinction decreases with the number of species. In contrast, the intertemporal value of protection remains constant. Where these functions cross defines the point below which protecting the species pool becomes the optimal management strategy. This proof holds true for any two functions whose difference is increasing in s_t.

protecting is optimal (see Proposition 3 in Supporting Information 1, section 1.4). We obtain a general, closed-form solution for this threshold $\bar{s}$, which characterises the level of biodiversity protection that maximises net ecosystem service value over all periods given uncertainty. Performing comparative statics, we determine how $\bar{s}$ depends on the costs, discount factor, number of critical species, and service's value (Supporting Information 1, section 2). To check the analytical solution, we also solve this problem numerically, using value iteration (Bertsekas 1995; see Supporting Information 2: Part 1 for R code).

Multiple services

We next ask: under what conditions does managing for multiple services raise the optimal number of species to protect in comparison to managing for a single service? Multiple services could increase optimal protection levels by increasing the overall value of services or by increasing the number of critical species when different species provide different services (Hector & Bagchi 2007; Zavaleta *et al.* 2010; Isbell *et al.* 2011; Gamfeldt *et al.* 2013). To test these premises, we extend the single service model where all k critical species are required to provide a service. We consider two scenarios: (1) the same subset of species provides two services, and (2) two services are provided by non-overlapping subsets of species (Fig. S1). Since real communities likely fall between these extremes (Hector & Bagchi 2007), these scenarios bound the problem.

Different relationships between biodiversity and ecosystem services

We relax the assumption that the service requires all k critical species to be present, allowing the service level to increase with the number of species that provide it, i.e., considering immediate payoffs of the form $f(s_t, r_t) = v_r$ (here called the 'biodiversity-ecosystem service relationship'). We test the prediction that the shape of this relationship has important implications for species protection (Schwartz *et al.* 2000; Supporting Information 1, section 3). Based on previous empirical studies, we consider linear, convex, and concave relationships and represent the biodiversity-ecosystem service relationship using a flexible power function (following Reich *et al.* 2012; Mora *et al.* 2014; Liang *et al.* 2016; O'Connor *et al.* 2017). Here, this function is

$$v_r = ar_t^b, \tag{2}$$

where v_r *is* the service value generated by r_t service-providing species. We explore a wide range of published estimates for b in eqn 2 (Supporting Information 1, section 3.2) to reflect a range of assumed relationships, including linear ($b = 1$), concave or 'saturating' ($b < 1$), and convex or 'accelerating' ($b > 1$) (from Reich *et al.* 2012; Mora *et al.* 2014; Liang *et al* 2016; O'Connor *et al.* 2017). When $b > 1$, even small changes in the number of critical species can dramatically alter ecosystem service levels. In contrast, for $b < 1$, the level of a service will only change dramatically when few species remain (Schwartz *et al.* 2000). Most estimates of b reflect the relationship between species richness and ecosystem functions (i.e., standing stock biomass, *but see* Liang *et al* 2016), yet these parameter estimates provide a useful starting point here because parameters for the biodiversity-ecosystem service relationship *per se* are typically unknown (Ricketts *et al.* 2016).

For each relationship, we use a *value function iteration* numerical approach (Bertsekas 1995) to approximate the optimal policy, implemented in R (see Supporting Information 2: Part 2 for code and Supporting Information 1, section 3 for more details).

RESULTS

We find the level of species protection that optimises net expected ecosystem service value over time. Protection is optimal only at or below this threshold number of species; we call the threshold level of species $\bar{s}$. We find $\bar{s}$ for several scenarios, explicitly considering uncertainty, and show how it depends on the model parameters. First, we analytically derive $\bar{s}$ for the case where the service value depends on all critical species being present ($f(s_t, r_t) \in \{0, v\}$). Second, the threshold nature of the optimal protection strategy holds for all biodiversity–ecosystem service relationships considered (i.e., different forms of eqn 2). Third, we find conditions under which optimising net value for multiple services results in a higher $\bar{s}$ than for a single service. We first present the analytical results, followed by the extensions to multiple services and different biodiversity–ecosystem service relationships. $\bar{s}$ can be no, all, or an intermediate number of species, and we define conditions giving rise to each outcome, below.

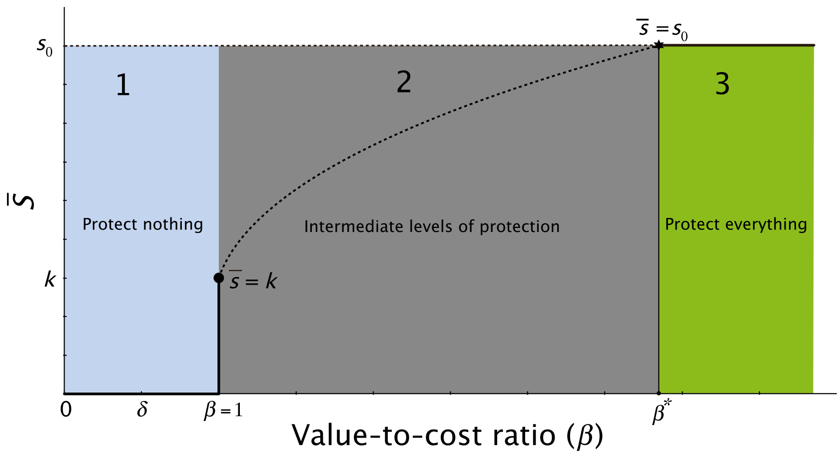

Figure 3 Graphical representation of the analytical solution (eqn 3) for the optimal number of species to protect. β is the value-to-cost ratio. $\bar{s}$ is the optimal protection level (in number of species); s_0 is the total number of species in the intact ecosystem, and k represents the number of species known to be critical to the service. β^* represents the value-to-cost ratio at which protecting the entire species pool is optimal eqn 3. In *Region 1,* no protection is optimal: the cost incurred by protection exceeds the services' value ($v < c$). When the value equals the costs ($\beta = 1$), protecting the bare minimum ($\bar{s} = k$) is the optimal policy. In *Region 2*, the value exceeds the costs ($\beta > 1$), so protecting more species than are presumed to be critical for the service is optimal: $\bar{s} = k$. As the value-to-cost ratio increases, the optimal protection level increases until protecting everything becomes optimal at β^* (given in eqn 4). *Region 3*: full biodiversity protection is always optimal when $\beta \geq \beta^*$.

Species protection level that optimises an ecosystem service: analytical solution

We analytically derive $\bar{s}$, the level of species protection (in number of species), for the case where service value is lost entirely if any k critical species are lost (for $f(s_t, r_t) \in \{0, v\}$) (using Theorem 1 and proving Proposition 3, see Supporting Information 1). To assist with intuition, we define $\beta \equiv \frac{v}{c}$, which is the ratio of value from the service to costs incurred by protection, and define $\bar{s}$ in terms of β to simplify the solution. The optimal protection level is the largest number of species satisfying

$$\bar{s} \leq \frac{k(\beta - \delta)}{(1 - \delta)}. \tag{3}$$

This solution for $\bar{s}$ is the number of species that maximises the net value of an ecosystem service over an infinite time horizon – which reveals the extent that an ecosystem service focus can provide an economic incentive for biodiversity protection.

Depending on the service's value relative to protection costs, several results emerge (Fig. 3). First, species protection is never optimal when the costs exceed the value (Fig. 3: Region 1). Second, as long as the value exceeds the costs, protecting more species than are known to provide the service is optimal ($\bar{s} \leq k$) because of uncertainty over which species are critical to protect to secure services over time (Fig. 3: Region 2). Third, for $s_t > \bar{s}$, protection is not optimal, even when the service's value exceeds the cost of protection, because the risk of losing the ecosystem service in the next period is sufficiently low that it does not economically justify investing in protection. If the service has already been lost, the optimal economic strategy is not to protect any species in the future, since this initial model does not consider the possibility to restore the service. Finally, under certain conditions of eqn 3, protecting all species is optimal, such that $\bar{s} \geq s_0$ (Figs 3, S2 and S3).

Because there is uncertainty over which species need protection to sustain an ecosystem service, solution (eqn 3) shows that is always optimal to protect more species than the number known to be critical for providing the service as long as: the service value exceeds the protection costs ($\bar{s} > k$, Fig. 3: Region 2) and the discount factor is < 1 [$\delta < 1$ implies a preference to obtain value now versus later (Arrow *et al.* 2013)].

The optimal level of protection $\bar{s}$ depends nonlinearly on the discount factor (Supporting Information 1, section 2). When the manager places no weight on the future ($\delta = 0$), $\bar{s}$ will be lower than the optimal level for a manager with greater emphasis on future values. For instance, when the service value is twice as large as the protection costs and 10 species are critical, $\bar{s}$ will be around 50 times higher with $\delta = 0.95$ than for a myopic level of protection with $\delta = 0$ (Supporting Information 1, section 1.3.4). Similarly, $\bar{s}$ decreases nonlinearly as the costs incurred by protection increase; whereas, $\bar{s}$ increases linearly with the service's value and with k (Figs S2 and S3; Supporting Information 1, section 2).

Economic criteria for protecting all species to be optimal

We find the conditions under which the optimal management for ecosystem services is protecting all species, by rearranging the analytical result (eqn 3). Protecting all species is optimal when the value-to-cost ratio, β, is equal to or exceeds a critical value defined as

$$\beta^* \equiv \delta + \frac{(1 - \delta)s_0}{k}. \tag{4}$$

If this criterion is met (i.e., when $\frac{v}{c} \geq \beta^*$), an ecosystem service focus can economically motivate full biodiversity protection (see Supporting Information 1, Proposition 4), bounding region 3 in Fig. 3. The level of β^* needed for protecting all species to be optimal (from eqn 4) drops nonlinearly as the fraction of species critical for the service (k/s_0) increases (Fig. 4), eventually equaling 1 when all species in the community are critical to the service ($k = s_0$). In comparison, increasing the discount factor (δ) linearly decreases β^* (Fig. S4; Supporting Information 1, section 2).

The fraction of total species directly critical for a service, k/s_0, can vary dramatically among services and ecosystems, with important consequences for the β^* that warrants full biodiversity protection. We plot empirical estimates of k/s_0 for 6 services and ecosystems (Fig. 4; Table S1). The observed differences in this small sample suggests that this β^* criterion is more likely to be met in some ecosystems than in others.

Considering multiple services can increase optimal protection levels

A threshold level of species protection is also optimal for multiple services (see Supporting Information 1, section 1.5, Proposition 6). We prove that this threshold is greater than or equal to the $\bar{s}$ from the most valuable single service when the two services (1) require a larger total number of critical species than required for each single service; and (2) the value produced from multiple services is greater than or equal to the most valuable single service (see Supporting Information 1, section 1.5, Proposition 7). When all services are provided by the same set of species, the problem reduces to the single service problem (i.e., solution eqn 3), albeit with a higher service value. For instance, accounting for both shoreline protection and carbon sequestration provided by mangroves increases estimates of overall service value (Barbier *et al.* 2011) and leads to more protection than would be optimal if considering either service by itself. When different species provide different services, although more species are considered critical, losing any one of them will result in only a partial loss of the total service value. Still, when the aggregate value produced by both services is higher, the optimal protection level will always increase relative to the level for either service alone (Supporting Information 1, section 1.5). The degree to which multiple services raise the optimal protection level depends on how single services combine to produce total value (e.g., synergistically, additively, or with trade-offs), how management and opportunity costs scale with the number of services, how the total value is distributed across services (e.g., *is one service much more valuable?*), and how much the critical species for different services overlap.

Optimal protection levels for different biodiversity-ecosystem service relationships

The same general conclusions arise for different relationships between the number of critical species (r_t) and the service's value, following $f(s_t, r_t) = v_r$ in eqn 2: no protection is optimal until the species pool (s_t) declines to a threshold number, $\bar{s}$. Each number of r_t species has a corresponding optimal level of protection $\bar{s}$ for a range of reasonable conditions (Figs 5, 6, and S5–S7, Supporting Information 1, section 3). Protecting species is never optimal ($\bar{s} = 0$) when costs outweigh the maximum value from the service (Fig. 5). As for solution

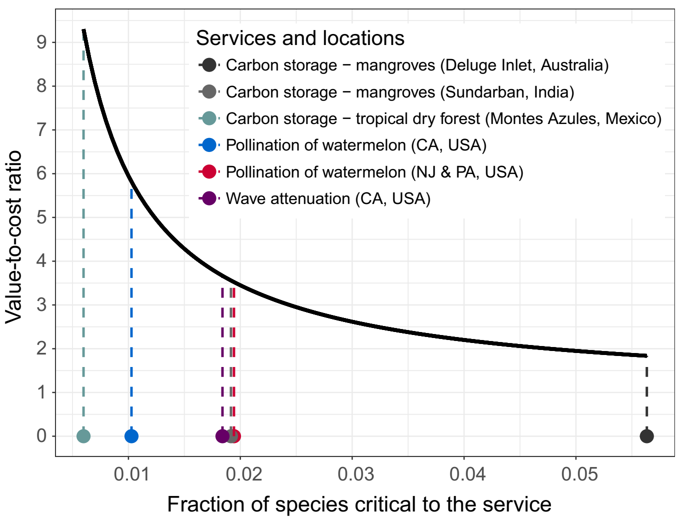

Figure 4 The economic criterion (in eqn 4) for protecting all species to be optimal depends heavily on the fraction of total species in an ecosystem that are critical to the service (k/s_0). The solid black line indicates ratio of value to costs (β^* given in eqn 4) where protecting everything is economically optimal as a function of k/s_0 for a discount factor of $\delta = 0.95$. When the fraction of critical species is small, the service value must be many times greater than the protection costs to warrant protecting all species. However, as the fraction of critical species increases, full protection is warranted even if the service value barely exceeds the protection costs. From empirical estimates of k/s_0, this approach can be used to determine how many times greater the services' value must be than the costs for protecting all species to be optimal, which we illustrate with several services and locations. Table S1 provides information and references for each example. When there was a range for the fraction of critical species, we computed and show an average fraction here (see Table S1 for more information). Note that the average fraction of critical species for pollination (NJ & PA, USA), carbon storage (Sundarban, India), and wave attenuation (CA, USA) are nearly overlapping (at 0.185–0.191).

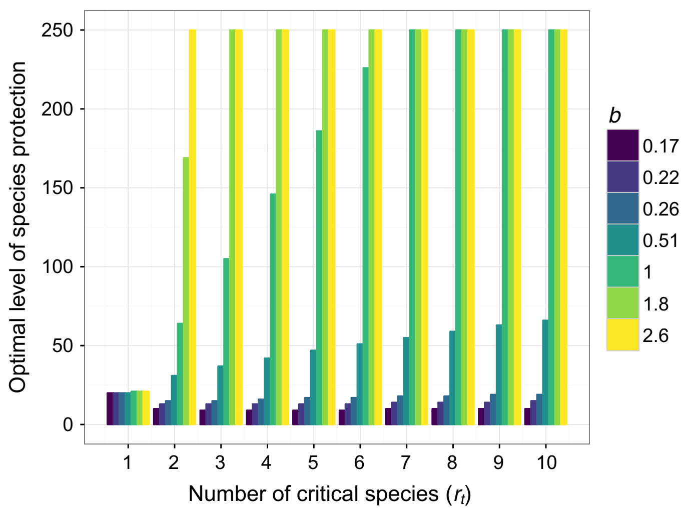

Figure 5 For each number of critical species r_t, there is an optimal protection level, $\bar{s}$. However, $\bar{s}$ depends on the shape of the biodiversity-ecosystem service relationship, as determined by the b parameter of the power function in eqn 2. This figure shows the optimal level of protection for different b parameter values, while holding the other parameters constant ($a = 20$, cost = 10, $s_0 = 250$, and $\delta = 0.95$).

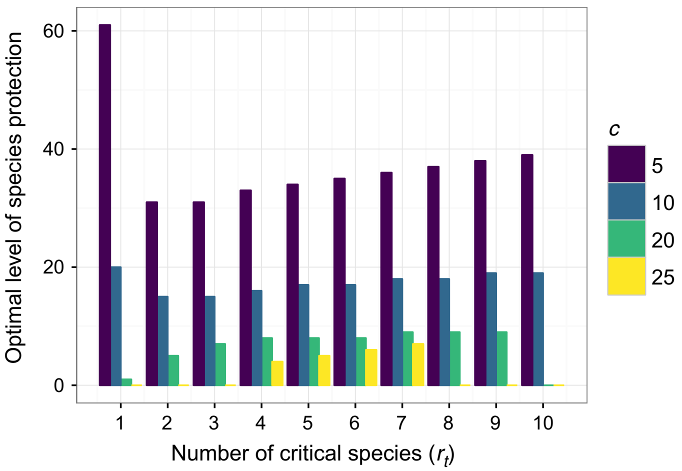

Figure 6 Certain curvatures of the biodiversity-ecosystem service relationship lead to interesting interactions with costs that determine the optimal protection level. This figure shows how different levels of costs affect the optimal protection level for a concave ('saturating') relationship, with $b = 0.26$, $a = 20$, $s_0 = 250$, and $\delta = 0.95$. First, the optimal protection level does not monotonically increase with the number of critical species (r_t). In some cost scenarios, no protection is optimal for certain levels of r_t (for an example, see $c = 25$). In other costs scenarios (e.g., $c = 5$ or 10), the highest level of protection occurs when only one critical species remains; for extremely concave relationships ($b <$ approximately 0.263), this result arises because the largest loss in value occurs when r_t goes from 1 to 0. Second, higher costs typically lead to lower optimal protection levels for a given r_t, a result that also holds for other b values (Fig. S7).

eqn 3, optimal protection levels decrease as decision-makers value the present more than the future (with lower δ) (Fig. S5) and as protection costs increase (Figs 6 and S6).

The optimal level of species protection greatly depends on the shape of the biodiversity–ecosystem service relationship (Fig. 5). Convex relationships ('accelerating curves' with $b > 1$ in eqn 2) typically result in more protection, holding other conditions constant. In contrast, concave relationships ('saturating curves' with $b < 1$) provide comparatively limited economic incentive for protection except in the exceptional case of extreme concavity when $r_t = 1$ (Fig. 5). With such complete substitutability (reflected in extreme concavity), the optimal protection level is low until only one service-providing species remains (with $b <$ approximately 0.263, Fig. 5) under certain costs (Fig. 6). This result arises because the largest incremental loss in value occurs when the number of critical species in the community transitions from $r_t = 1$ to $r_t = 0$. $\bar{s}$ also depends on the costs relative to the a parameter from eqn 2, and specifically their ratio (c/a), because costs and a affect $\bar{s}$ in the opposite way. Holding all else constant, the same c/a ratio leads to the same $\bar{s}$, regardless of the absolute costs and a (compare Figs 5 and S8).

DISCUSSION

Our theoretical analyses provide a framework for predicting when particular ecosystem services provide strong vs. weak economic incentives for biodiversity protection. We find two key and general results. First, we generally find it is optimal to protect more species than are known to be critical to a service, as long as the service's value exceeds the costs incurred by management; this is due to uncertainty over which species need protection to maintain ecosystem service over time. Second, the optimal species protection strategy, driven solely by net ecosystem service value, is to invest in protection when the number of remaining species declines to the critical threshold $\bar{s}$, provided that the ecosystem service is not lost (Figs 3 and 5). At $\bar{s}$, the potential costs of losing another species (in terms of lost current and future value from the service) exceed the costs of protecting the species pool. Therefore, once the number of species declines to $\bar{s}$, the value from protecting exceeds the expected value of not protecting (Fig. 2), and the optimal strategy is to protect all remaining species in perpetuity. We find the conditions when optimising net ecosystem service value results in protecting no species, protecting all species, and cases in between (Figs 3, 5 and 6).

The results provide analytical insight into the degree to which conservation outcomes can be achieved solely through efforts targeting the net value of some ecosystem services. We find the level of species protection that is optimal for net ecosystem service value, $\bar{s}$, for several cases. In the extreme, protecting all species can be economically optimal if the ratio of service's value to costs incurred by protection equals or exceeds β^* given in eqn 4 (Fig. 3: Region 3). For all value-to-cost ratios below β^*, managing solely for some ecosystem services will leave species at risk of functional extinction (Fig. 3: Region 1). Together, these criteria define cases where an expanded toolbox of policies and management approaches (e.g., endangered species regulations) will be required to protect biodiversity even when optimally managing for some ecosystem services. Several implications for decision makers and avenues for future research emerge.

The number of species critical to services influences conservation outcomes

The value-to-cost ratio, β^* in eqn 4, that would promote full biodiversity protection is strongly dependent on the fraction of species in the ecosystem that play a critical role in providing the service (Fig. 4). This result prompts important empirical questions: how large or how consistent is this fraction across services and locations? A growing body of empirical research addresses this question, estimating fractions of the species required to sustain one or more services in natural and experimental systems (e.g., Balvanera *et al.* 2005; Isbell *et al.* 2011; Fauset *et al.* 2015; Kleijn *et al.* 2015). For instance, Balvanera *et al.* (2005) estimated that 13% of tree species stored 90% of carbon in a tropical dry forest. Similarly, Zedler *et al.* (2001) found that 5 or fewer species out of a total of 163 in a salt marsh provided the bulk of coastal protection (Hechinger *et al.* 2011). Across other systems, empirical studies in natural ecosystems suggest that the fraction of species directly contributing to service provisioning varies but in several cases is relatively small (< 20%; Table S1). When such empirical estimates are available, our analytical results in eqn 4 provide a criterion defining how much greater the value of the service needs to be relative to protection costs to warrant full biodiversity protection based on the net value from a single service (Fig. 4; Table S1). This criterion will vary across services and locations based on details about how many species provide the bulk of services, relative to the total number of species. For certain k/s_0, full biodiversity protection is economically optimal if the service value equals the protection costs. Yet, in the six illustrative case studies we examined, the value of these services must exceed the cost 2 to 9 fold to justify full biodiversity protection (Fig. 4; Table S1). However, additional research is needed to determine these fractions of critical species when considering longer time horizons, larger spatial scales, and changing environmental conditions.

Another research frontier is determining the number of and which species are indirectly critical. Species interactions undoubtedly alter how many and which species are required to maintain services (Kremen 2005; Bohan *et al.* 2016; Dee *et al.* 2017). This model did not account for non-obligate species dependencies or the possibility of secondary extinctions following functional losses of species (Dunne *et al.* 2002). Integrating species interactions into the framework may dramatically increase the number of species indirectly needed to sustain ecosystem services, which would lower the β^* criteria. Extending the framework to include dependencies among species, and the potential for cascading extinctions, is a promising area for future research.

High costs dramatically reduce optimal protection levels

Increasing the costs of protecting species (either opportunity costs or direct costs of management) decreases the anticipated amount of biodiversity protection afforded by management for ecosystems services (Figs 6, S3 and S6). Such costs vary widely by location. For example, opportunity costs can be influenced by whether land is privately versus publically owned. For private lands, alternative land uses are often less restricted, which increases opportunity costs. For example, in tropical forests of Southeast Asia, profitable oil palm (*Elaeis guineensis*) plantations and logging create relatively high opportunity costs (e.g., for Borneo, Butler *et al.* 2009; Fisher *et al.* 2011). When opportunity costs grow, ecosystem services need to be even more valuable to incentivise protecting species. Zoning critical areas on land or in the ocean that provide important services is one regulatory means of reducing opportunity costs.

The clear impact of costs on the level of biodiversity protection also highlights the value of reducing the direct costs of species protection (Figs 3 and 6). Gains in efficiency that protect species at lower costs (e.g., identifying and reducing threats more strategically – Wilson *et al.* 2007; Helmstedt *et al.* 2016) would significantly enhance levels of biodiversity protection warranted by net ecosystem service value.

Payment for ecosystem services can enhance protection

Increasing the financial value of services relative to conservation costs will increase how much biodiversity protection is optimal (Figs 3 and S3; see eqn 3 and Supporting Information 1, section 2). One way to increase the service value is supplementing the market value for services with payment for ecosystem services (PES) programs. Solving for the value-to-cost ratio, β^* in eqn 4, can help define how much added value a PES program must assign to services to promote economic incentives for full biodiversity protections. For instance, REDD+ aims to compensate landowners for maintaining tropical forests that sequester carbon. Since carbon credits are currently less valuable than the opportunity costs from alternative uses such as logging or oil-palm plantations, studies predict that PES programs cannot compete (Butler *et al.* 2009; Fisher *et al.* 2011; *but see* Abram *et al.* 2016). Our model can help estimate how much higher payments need to be to foster full or a target level of biodiversity protection. We illustrate the potential utility of criteria from the analytical solution by calculating β^* for protecting all species ($\bar{s} = s_0$), yet an analogous ratio could be calculated for any other target level of biodiversity protection ($< s_0$) desired by society by rearranging eqn 3.

Are the species providing services at higher or lower risk of functional extinction?

Our model assumes that without protection, species will be lost at random; this follows most experimental work on biodiversity and ecosystem functioning (e.g., Hector *et al.* 1999; Tilman *et al.* 2001). However, in natural systems, species' extinction risks differ, thus functional extinctions are non-random (Pimm *et al.* 1988; Smith & Knapp 2003). Considering non-random species losses would change our results about the optimal level of protection in predictable ways. First, if services were provided disproportionately by species at the greatest risk of extinction, our results provide a lower bound for optimal protection. In contrast, several studies on regulating services (pollination and carbon storage) suggests that abundant species, at lower risk of functional extinction, provide the bulk of services in natural systems, at least under current conditions (e.g., Fauset *et al.* 2015; Kleijn *et al.* 2015; Winfree *et al.* 2015). Under these circumstances, our results provide an upper bound for optimal biodiversity protection. An important area for future research is determining whether the species able to contribute the most to ecosystem services also face the greatest risk of functional extinction. This agenda should examine the roles of dominant versus rare species in services and whether a species' extinction risk and its relative contribution to services are positively or negatively related.

Biodiversity-ecosystem services relationships and optimal species protection

Previous studies posit that the shape of the biodiversity-ecosystem service relationship will influence how much species protection is optimal for ecosystem services (Schwartz *et al.* 2000). Our results explicitly test and support these assertions. When the relationship between biodiversity and ecosystem services saturates more quickly (i.e., for lower b values in eqn 2 when $b < 1$), we typically find less protection is optimal, as expected (Fig. 5). The highest level of species protection, holding all else constant, results from the case where all k critical species are needed to obtain the service; therefore, the analytical solution in eqn 3 bounds the results.

Empirical estimates describing relationships between biodiversity and the level of service value are not currently known for most ecosystem services (Ricketts *et al.* 2016; *but see*

Liang *et al.* 2016). Our results show that assuming the wrong relationship, and making species protection decisions for ecosystem services based on that incorrect assumption, would result in losses in both ecosystem service value and species (i.e., assuming a saturating relationship when, in fact, the relationship is linear). Further, as costs increases, the difference between the optimal level of species protection for a convex ($b > 1$) vs. concave ($b < 1$) relationship becomes larger for a given a in eqn 2 (Fig. S6). These findings highlight the need to improve empirical estimates of these relationships at management-relevant scales, particularly in contexts with high management and opportunity costs. These empirical estimates can then be integrated into our approach.

How much does managing for multiple services increase optimal species protection levels?

Considering more than one service can increase the number of species that are optimal to protect relative to a single high value service, but not always. Counterintuitively, when different species provide different services, the optimal protection level will not necessarily be higher than when the same species provide more than one service. This result arises because, when different species provide different services, the loss of any one additional species only results in partial loss in service value. The extent that managing for multiple services raises the optimal protection level relative to single services depends on several factors – some with currently limited empirical data for most ecosystems. Unresolved questions for future work include the extent of overlap in critical species shared across services; whether subsets of species providing different services differ in extinction risk; how the cost of protection scales with the number of services being targeted; and whether managing for one service provides benefits to another because subsets of species providing different services require the same management interventions.

Uncertainty and the value of information

We find that protecting more species than are known to be critical for services is optimal when there is uncertainty over which species are critical for specific services and which species will be functionally lost without protection. New research could identify which species are critical to protect for services and reduce the costs of maintaining a service. Ironically, although lower costs for biodiversity protection would normally enhance the optimal level of protection (Fig. 3), better insight into which species are critical to protect can reduce incentives from uncertainty to protect non-critical species. However, this study considered only two types of uncertainty. Other sources of uncertainty may also influence the outcome (e.g., uncertainty over value, costs, and the number of critical species) and warrant further attention (Hamel & Bryant 2017; Runting *et al.* 2017). Scientific research can reduce uncertainties associated with managing for ecosystem services. Therefore, extending our approach to quantify the value of information (e.g., see Raiffa 1968; Canessa *et al.* 2015; Williams & Johnson 2015), future research could address: What is the value of such new information in terms of service value and in species conserved?

CONCLUSIONS

Our theory quantifies the conditions when optimising net value of ecosystem services will benefit all biodiversity and when it will not. Analytically, we find the conditions under which ecosystem services provide a sufficient economic incentive for protecting all species, when they justify protecting nothing, and cases in between. We show how the amount of protection that is economically justified depends on (1) the benefits from the service relative to the direct and indirect costs of conservation, (2) the number of critical species and services involved, (3) how decision-makers value present vs. future benefits (i.e., discounting), and (4) uncertainty over which species provide benefits and which will be lost. For instance, uncertainty about which species are critical to protect for services raises the level of optimal biodiversity protection, while increasing opportunity costs reduces the level of biodiversity protection.

Biodiversity can be critical to services. Nevertheless, a focus solely on the net value of ecosystem services might still leave large fractions of biodiversity unprotected across a range of scenarios. This theory explores the conditions that must hold for ecosystem services goals to provide economic incentives for full biodiversity protection in the face of uncertainty. As a result, it bounds the conditions when other policies or management actions will also be needed to provide high levels of both ecosystem services and biodiversity preservation.

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AUTHORSHIP

LD conceived of the project and research question; LD and CC formulated the problem and model framework; LD and MDL performed the analytical analyses; MDL provided the technical lemmas; LD performed numerical analyses and wrote the R code; LD wrote the paper with input from all authors.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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