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Managing ecosystem services in the face of uncertainty: what is the role of biodiversity?

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Environmental Science & Management

by

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Forthcoming peer-reviewed publications

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ABSTRACT

Managing ecosystem services in the face of uncertainty: what is the role of biodiversity?

by

Laura Ellen Dee

The conservation community is increasingly focused on managing nature explicitly for ecosystem services that provide benefits to humans, rather than for its intrinsic value. Though often debated, the consequences of conserving ecosystems for their services rather than for the explicit goal of biodiversity protection are not clear. While biodiversity can contribute to ecosystem services, this scientific link is fraught with uncertainty. How many and which species to protect is thus an important challenge for applied and theoretical environmental science, as well as new policy initiatives, such as the intergovernmental platform on biodiversity and ecosystem services (IPBES).

My first chapter presents new theory to address the extent to which a goal of ecosystem service provision creates a significant economic incentive for biodiversity protection when facing uncertainty over how biodiversity produces services. I derive the level of biodiversity protection that maximizes ecosystem service provision under uncertainty and define a criterion that can be used to determine when managing for ecosystem services economically justifies broad-scale biodiversity protection. I

illustrate the utility of this criterion, applying it to several ecosystem services across locations (pollination, wave attenuation, and carbon storage).

Next my second chapter considers factors other than uncertainty that may increase alignment between management to obtain ecosystem services versus explicitly to conserve biodiversity. I find the objectives of conserving biodiversity and delivering ecosystem services align more frequently than would be predicted by considering only the known and direct contributions of abundant species to current ecosystem service provisioning. Specifically, I review existing literature on four factors that strengthen alignment, finding the following. First, the number of species that contribute significantly to services is much larger than many current estimates from observational studies. Second, coarse management actions to enhance ecosystem services, such as protecting a location or restoring a habitat type, can provide “incidental” conservation benefits at no additional cost. Third, managing for services should provide broader benefits to biodiversity by disproportionately protecting at-risk species if the species most at risk of local extirpation also contribute significantly to one or more services (i.e., rare or threatened species). Fourth, managing for even a single, relatively low value ecosystem service can have indirect benefits to biodiversity if the species that are significant to service provision have functional ecosystem roles that promote biodiversity (e.g., if they are habitat forming species or keystone predators). However, significant uncertainty remains, especially surrounding the service provisioning roles of the vast number of rare species in nearly every ecosystem.

Finally, in my third chapter, I aim to reduce uncertainty about the role of biodiversity in the provision of a specific ecosystem service (fisheries yields) in variable climates. I develop theory to predict the consequences of within-year temperature variability for yields and explore the role diversity might play in offsetting potential impacts. I hypothesize that higher functional diversity (FD), measured with traits related to species' responses to temperature, can mitigate impacts from temperature variability on yields. Using a global marine fisheries dataset, I find that within-year temperature variability reduces yields but current FD of targeted species largely offsets this effect, avoiding annual losses of 8% on average globally relative to if FD were degraded to the lowest level observed in the data.

All together, this dissertation contributes our understanding of when management strategies targeting ecosystem services versus biodiversity conservation align or when they do not. This knowledge is critical to new policies initiatives like IPBES with the dual of objective of protecting biodiversity and benefits nature provides people.

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I. To what extent do ecosystem services motivate protecting biodiversity?

Abstract

Society is increasingly focused on managing nature explicitly for ecosystem services rather for its intrinsic value. While biodiversity contributes to ecosystem services, this scientific link is fraught with uncertainty, so how many and which species to protect is an important challenge for applied and theoretical environmental science. We derive the economically optimal biodiversity protection strategy that maximizes ecosystem service provision under uncertainty. We explicitly consider biodiversity as an input into the production of services and use stochastic dynamic optimization to solve for an economically optimal protection strategy over time. While the typical result supports an intermediate level of biodiversity protection, we derive the conditions under which the economically optimal strategy is either complete biodiversity protection or no protection at all. We show how the optimal biodiversity protection strategy depends upon the relationships between species and services, including the consideration of multiple services. Moreover, we find that uncertainty surrounding how biodiversity produces services enhances the economic incentive to protect more species than presumed to be critical. We provide and illustrate the utility of simple criteria that can determine when managing for ecosystem services alone will economically warrant broad-scale biodiversity protection. When applied to empirical estimates, the criteria vary among services and suggest managing for ecosystem services alone will frequently provide limited protection for the entirety of biodiversity in some ecosystems. In such cases,

protecting biodiversity for its intrinsic value will require policy measures that extend beyond the concept of ecosystem services.

Introduction

Many conservation organizations and scientists have argued for a shift in focus from preserving biodiversity for its own sake towards protecting biodiversity for the values and benefits it provides to society – known as ecosystem services (1–6). Rather than pitting biodiversity protection against economic goals, the notion of valuing ecosystem services posits that the interests of humans and biodiversity conservation are often aligned (4, 7), because biodiversity can play a key role in producing ecosystem services (6, 8–12), and the value of these services can be large (13, 14). This suggests that protecting biodiversity is crucial to maintaining ecosystem services and that biodiversity's benefits extend beyond its intrinsic value (13). While significant time and effort have been devoted to addressing whether biodiversity positively impacts ecosystem services, an equally important, but unresolved question is whether maintaining ecosystem services provides a significant economic incentive for broad biodiversity protection (3, 15–18). If conservation decisions were based solely on optimizing the value of ecosystem services, how much protection of biodiversity would arise?

Determining when and to what extent managing for ecosystem services will result in an economic incentive for biodiversity protection requires carefully considering two factors. First, only a subset of biodiversity will be responsible for providing any single ecosystem service, which might mean protecting relatively few species could secure services. Second, our understanding of the link between biodiversity and services is riddled with uncertainty (11). The details of the roles played by different species, functional traits, and genes in producing services are typically poorly understood (19–21), especially under global change scenarios (9, 26). For instance, it is often unclear how results from small-scale studies that measure ecosystem function (e.g., biomass production) translate to large-scale ecosystem services (e.g., marketable crop production or reduced costs and inputs of fertilizers or pesticides) (21–25). Such uncertainty creates challenges for decision-makers tasked with managing biodiversity to secure ecosystem services.

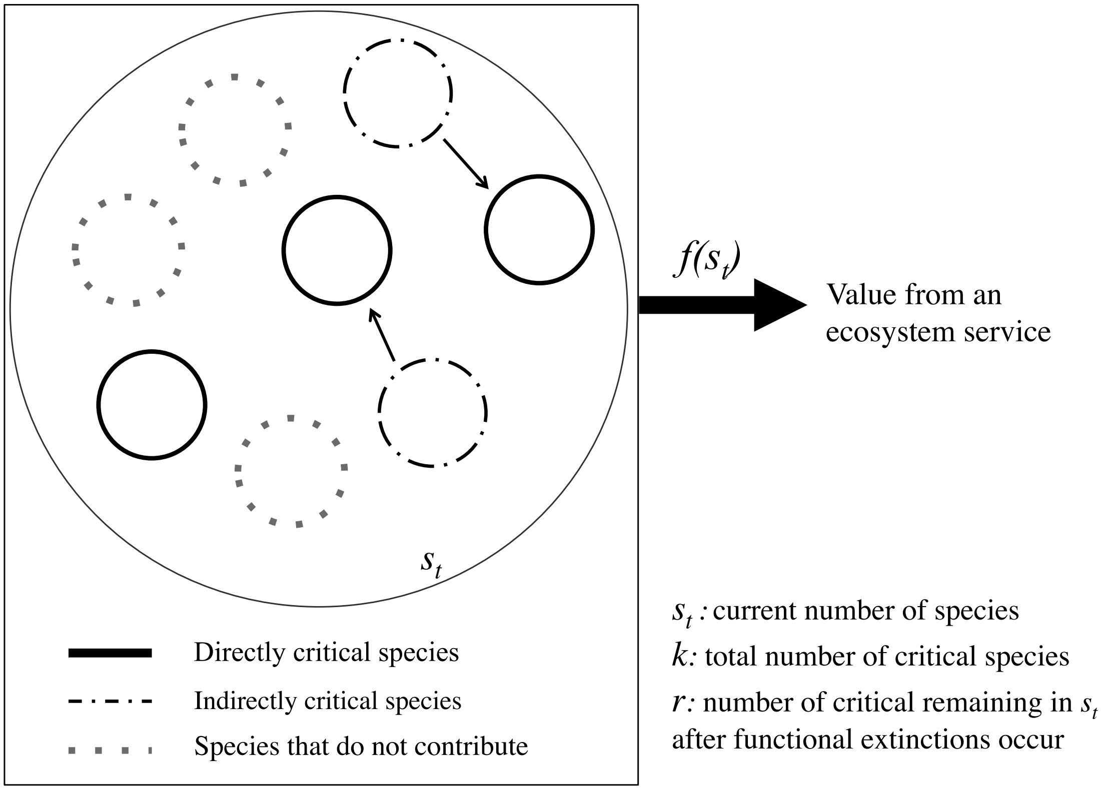
Here we develop an analytical framework to determine when decision-makers seeking to secure ecosystem services should invest in species protection given uncertainty surrounding the link between biodiversity and ecosystem services. Using this framework, we address several interrelated questions, such as: How many species are critical to protect to ensure the greatest expected value of services? Does uncertainty about which species are critical to services lead to less motivation for preservation (e.g., because many species may play no significant role) or greater motivation (e.g., because the value of lost services could be far greater than the cost of protecting species that unknowingly play no functional role)? And, how does the number of species providing a service affect the amount of biodiversity protection that will result from efforts to maintain the ecosystem service? Our analysis yields an economic criterion that can be applied broadly to shed light on when optimizing ecosystem services can also lead to broad-scale biodiversity protection, and we illustrate its utility for 7 ecosystem services.

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 level of ecosystem services (in $) over time (i.e., the ‘optimal protection level’) in the face of uncertainty over which species need protection to secure services. Although the intrinsic value of biodiversity (26) can be considered a service itself, we focus solely on the value of biodiversity as a dynamic and uncertain input into the production of other ecosystem services in contrast to many previous approaches that consider biodiversity and ecosystem services as distinct management objectives (18, 27, 28). We formulate a model informed by current knowledge about how biodiversity contributes to ecosystem services (10, 11) using tools from economics and control theory. We use biodiversity to refer to species diversity, but the framework could also apply to genetic or functional diversity.

We consider communities that are made up of two broad types of species: those critical to providing an ecosystem service (either directly or indirectly), and those that do not contribute to provision of 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; thus, managers face a challenge of incomplete information. For example, changes in climate and biogeochemical cycles may alter the plant species that contribute most to grassland ecosystem services (29). 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) in the absence of active protection. In disturbed habitats, species face some perpetual threat of functional extinctions, such as from habitat loss, disease, overexploitation, and climate change (30, 31). Our model accounts for both incomplete information over which species provide services for all time periods and uncertainty over which species will be functionally lost (random losses).

Figure 1. A 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 financial value for humans. For most services, considerable uncertainty remains over how species pools map to value from 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 (see *Methods*). 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 (32). Failing to protect has no direct financial cost, but inaction risks the loss of a critical species (and thus the service). Therefore, maximizing the net value of ecosystem services over time requires balancing the costs of protection with the current and future value of maintaining services.

To determine the optimal biodiversity protection strategy for ecosystem services, our theory bridges methodological and conceptual gaps between ecology and economics. Currently, most economic or ecosystem service production models treat the environment either as a single input into the production of services (33) or in terms of proxies such as habitat area (25, 34). Even more commonly, biodiversity is considered the objective to be maximized (to protect its intrinsic value or for bioprospecting of genes) rather than as an input in the production of other services (2, 18, 20, 27, 35). Instead, we explore the consequences when the only value of biodiversity is as a dynamic input to the production of services – meaning the number of species determines the level of a service, and decisions about species protection are driven solely by the motive of optimizing the net value of the service (see *Methods)*. We model cases where the current and future value arising from ecosystem services depend on the presence or number of critical species persisting in the species pool (8, 10, 11). We derive the optimal sequence of decisions to protect species or not given the motive of maximizing net service values.

We consider several relationships representing how the current period payoff from an ecosystem service, $f(s_t)$, depends on the number of critical species providing it (8, 10, 29, 36–38). We introduce the model with an extreme case where the functional loss of any of the critical species causes complete and irreversible loss of the ecosystem service (i.e., $f(s_t) \in \{0, v\}$). We then explore cases that more closely mimic empirical studies of ecosystem functions, where the service level decreases in a linear (38), convex (39), or concave (10, 36) fashion with the loss of species providing it following $f(s_t,r) = v(r)$, where r is the number of remaining species that contribute to the service (see *SI*). For each case, we derive the optimal sequence of decisions to protect species or not given the motive of maximizing net service values.

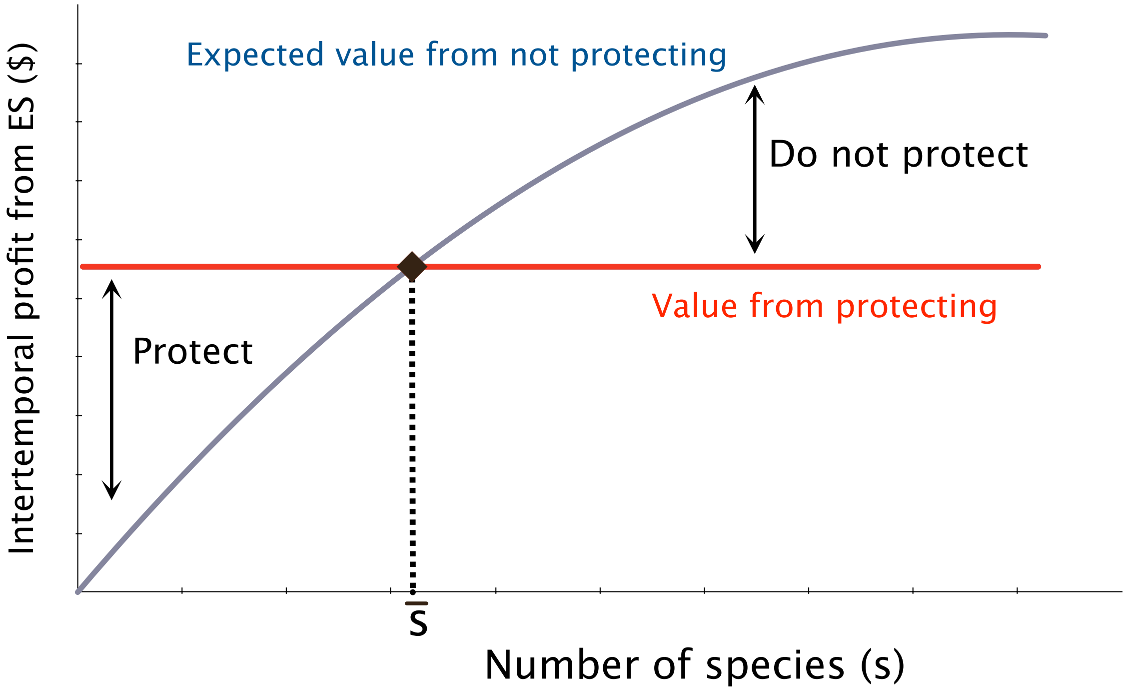
We assume that: **1)** the immediate service value, $f(s_t)$, is known and quantifiable (in \$) at each level of diversity; **2)** species losses are random and do not lead to cascading secondary extinctions (as supported by (40, 41)) and **3)** when species protection is pursued, it is successful but incurs a financial cost, c. This cost has two known components: the direct cost of protection and the opportunity cost of values forgone from activities that must be banned or reduced to provide species protection (e.g., exploiting species, developing land, etc., (32)). We conservatively restrict the decision-maker's actions at any time to no protection or protection of the species that is under threat of functional extinction in the current period. The community begins with s_0 species, k of which are critical to the ecosystem service (Fig. 1). At any later time t, s_t denotes the remaining number of species and r is the number of critical species that remain after some are functionally lost. The discount factor, δ, represents how heavily the future is weighted relative to the present: $\delta = 0$ implies a preference to obtain value only in the present, while the present and future are weighted equally when $\delta = 1$ (reviewed in (42)).

We derive the level of biodiversity protection (the "optimal policy") that maximizes the net ecosystem service value over an infinite time horizon using Stochastic Dynamic Programming methods (*Methods* & *SI*; (43, 44). Different levels of species protection (i.e., all species, no species, or intermediate numbers of species) optimize value from ecosystem services under different conditions, which we derive analytically. We then determine how the optimal number of species protected scales with the number of species that deliver a service, the costs associated with species protection, multiple services, and the relationship between the number of service providing species and the value of the service.

Results

The optimal policy of biodiversity protection driven solely by ecosystem service objectives is to start investing in biodiversity protection when the number of remaining species declines to a critical threshold, provided that the ecosystem service has not been lost. This threshold represents the financially optimal protection level, denoted $\bar{s}$, which is the number of species that will maximize the net service value over time. Once the size of the species pool declines to this threshold, the value of protecting exceeds the expected value of not protecting (Fig. 2; *Methods*), and the optimal decision is to protect all remaining species in perpetuity. However, biodiversity protection may still not be economically justified, even when the service value exceeds the cost of protection. For species pools larger than $\bar{s}$, the risk of losing the ecosystem service is sufficiently low that it does not make economic sense to bear the costs of protection. Therefore, if there is little risk of losing the service in the next period, there may be no incentive to bear the costs of protection. If the service has already been lost, then the optimal economic policy is not to protect any species in the future, since we are ignoring the possibility of restoring the service in this initial model. Similarly, ecosystem services never provide an economic incentive for species protection when the value of the service is less than the costs of protection.

Figure 2. An illustration of the intuition behind the mathematical proof that finds the optimal policy. It compares the inter-temporal value of the service arising from protecting versus the expected value from not protecting as a function of the number of species (s_t), conditional on still having the service after species are functionally lost. 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 inter-temporal 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 in increasing in s_t.



The threshold nature of economically optimal protection holds for all relationships between payoffs from an ecosystem service and the number of critical species that we considered (i.e., the forms of $f(s_t)$). For example, consider the introductory case where service value is lost entirely with the loss of any one of the k critical species ($f(s_t) \in \{0, v\}$). To assist with policy intuition, we define the optimal protection level in terms of the ratio of value received from the service to costs incurred by protection (which we call β; $\beta \equiv \frac{v}{c}$). The optimal protection level is the largest number of species satisfying

$$\bar{s} \leq \frac{k\,(\beta - \delta)}{(1-\delta)}. \qquad \textbf{[1]}$$

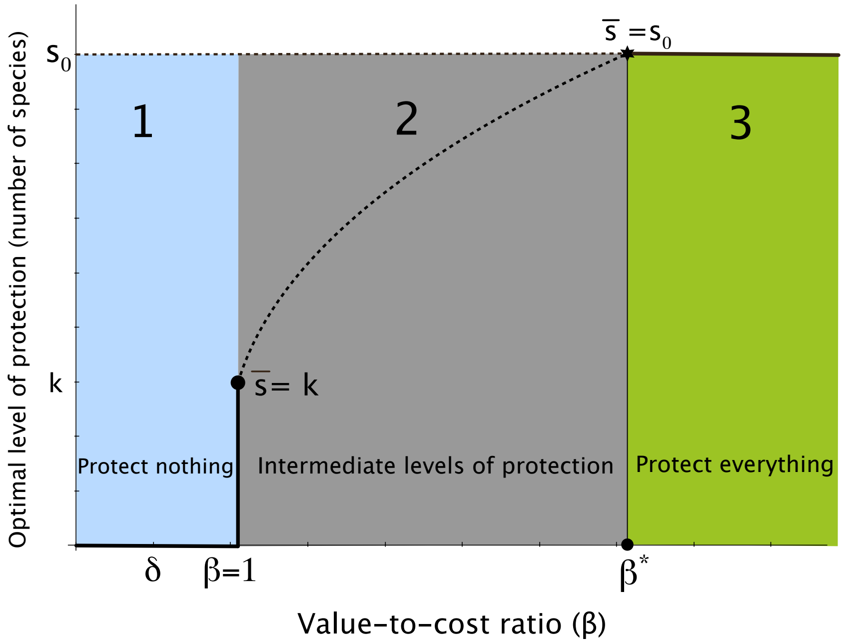
This solution for $\bar{s}$ is the number of species that maximizes the net value of ecosystem services over time. It reveals the extent that ecosystem services alone provide economic incentives for biodiversity protection.

Special cases of this solution exist under which it is optimal to protect all species or no species (Fig. 3). Protecting all species is optimal when the ratio of value-to-costs is equal to or exceeds a critical value of β, defined as

$$\beta^*(s) \equiv \delta + \frac{(1-\delta)\,s_0}{k}. \qquad \textbf{[2]}$$

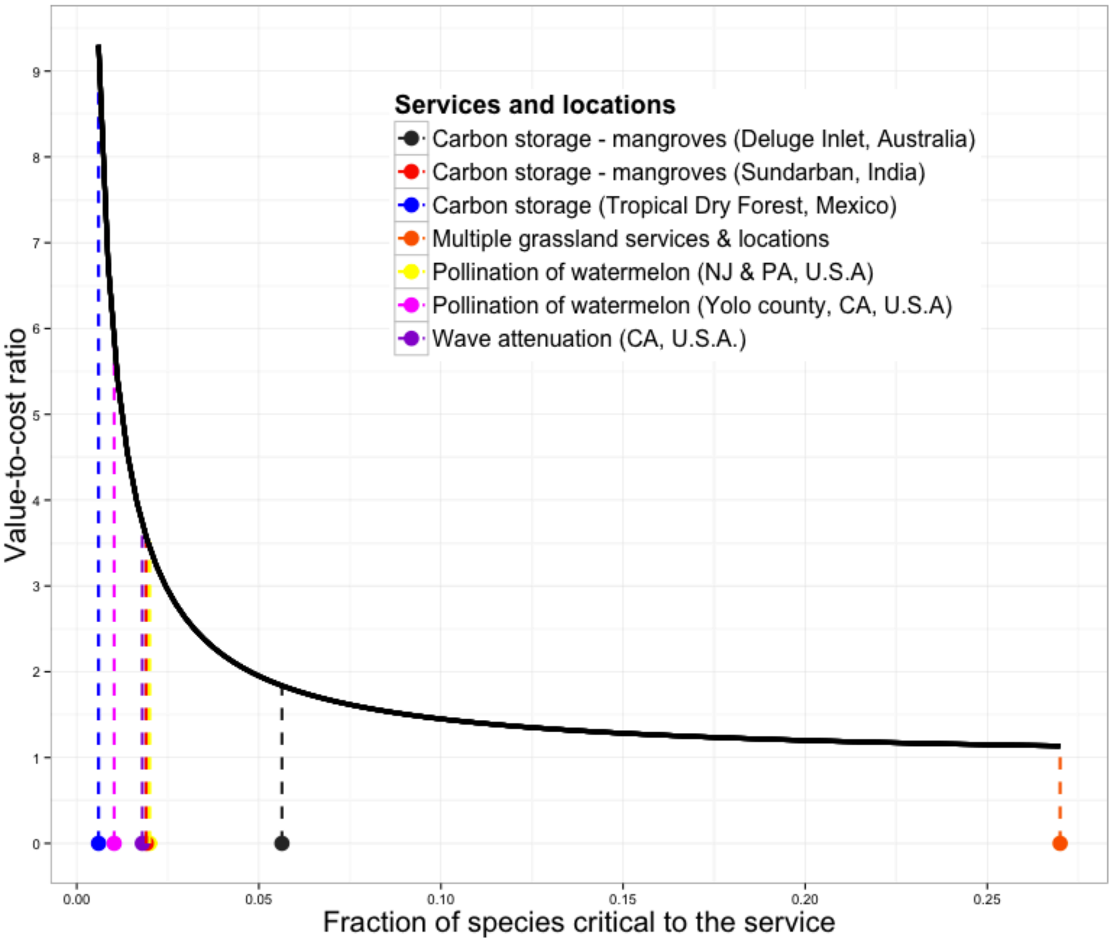
This condition bounds region 3 of Fig. 3. If this criterion is met (when $\frac{v}{c} \geq \beta^*$), ecosystem services can economically motivate full biodiversity protection.

Figure 3. Graphical representation of the analytical solutions **[1&2].** β is the value-to-cost ratio, $\bar{s}$ is the optimal protection level, 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. In **Region 1,** no protection is optimal: the cost incurred by protection exceeds the services' value ($v < c$). When the value equals the costs (β =1), protecting the bare minimum ($\bar{s} = k$) is the optimal policy. In **Region 2**, the value exceeds the costs (β > 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*. **Region 3:** full biodiversity protection is always optimal when β ≥ β*.



As the fraction of species that are critical for the service (k/s_0) increases, the critical ratio of service value to protection costs (β*) needed for protecting all species drops non-linearly to a value of 1 (*Fig. 4*). The fraction of species directly critical for a service can vary dramatically among services and ecosystems, with important consequences for the economic conditions that warrant full biodiversity protection. We plot empirical estimates of the fraction of species that are directly critical for 7 services/ecosystems (*Fig. 4; SI Table 1*). The observed range of variation in this small sample suggests that the operational criterion for full biodiversity protection ($\frac{v}{c} \geq \beta*$) is far more likely to be met in some ecosystems than in others.

Figure 4. The ratio of value to costs (β*) where protecting everything is economically optimal as a function of fraction of species that are critical to the service (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 multiples of 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 to warrant protecting all species, which we illustrate with several services and locations. When there was a range for the fraction of critical species, we computed and show an average fraction here. *SI* Table1 provides information and references for each example. Note that the average fraction of critical species for pollination (New Jersey & Pennsylvania, U.S.A.), carbon storage (Sundarban, India), and wave attenuation (California, U.S.A.) are nearly overlapping (0.185-0.191).



Because there is inevitably uncertainty over which species are required to provide an ecosystem service, it 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 costs of protective action (*Fig. 3: Region 2* where $\overline{s} > k$) and the discount factor is less than 1 ($\delta < 1$ implies a greater preference to obtain value now versus later, which is widely considered true (42)). When the manager places no weight on the future ($\delta = 0$) and acts myopically, the level of protection will be lower than the optimal level with greater emphasis on future values. For instance, when the service value is twice as large as the costs of protection and 10 species are critical, the optimal level of protection will be approximately 50 times higher than an extremely myopic level of protection (*SI 1.3.4*).

The same general conclusions arise when we relax the assumption that the service depends on all k species being present. When the level of the service increases smoothly with the number of species providing it ($f(s_t) = v(r_t)$), it is still never optimal to protect species when costs outweigh the maximum value from a service (SI). When the value exceeds the costs, the optimal policy is no protection until the species pool (s_t) declines to a critical threshold number. At this size species pool (s_t), which includes the r_t remaining species that provide the service, the potential costs of losing another species exceed the costs of protection. Each number of r_t species has a corresponding optimal level of protection $\overline{s}$ (*Fig. S5*) for a range of reasonable conditions (*SI*). Again, the more society values the present versus the future and the greater the costs of protection, the lower the optimal protection level.

Varying the functional form of the relationship between the number of critical species and the level of the service received (e.g., linear, concave or convex) revealed that convex relationships where the service value declines more precipitously in response to the loss of the initial key species typically result in more protection, holding other conditions constant. Concave relationships provide only limited incentives for protection except in the limiting case of extreme concavity. With such complete substitutability (extreme concavity), the optimal protection level is low until only one service-providing species remains. The appendix presents broader results for several non-decreasing relationships between service value and the critical number of species (*Fig. S5, S6*).

Extension of the framework: managing biodiversity for multiple ecosystem services

Ecosystems commonly provide multiple services. Does the presence of multiple services raise or lower the optimal number of species to protect? By extension of the single service model, multiple services could increase the optimal level of protection in two ways: by increasing the overall value of services and/or by increasing the number of critical species (29, 45, 46) when different species provide different services (12, 29, 46). We test these premises by considering two extremes for how multiple services could be provided by a community: full or no overlap in the species required for their provisioning. In reality, most services likely fall between these extremes (48). When all services are provided by the same set of species, the problem reduces to the single service scenario (i.e., solution [**1**]), 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 (47). This leads to more protection than would be optimal from either service by itself.

At the other extreme, each service could depend on non-overlapping subsets of species (12); *Fig. S1*). Then, although more species may affect service values, losing any one of the critical species will result in only a partial loss of the total service value. In such cases 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 (*SI*). In general, the degree to which multiple services raise the optimal protection level varies dramatically depending on how single services combine to produce total value (e.g., synergistically, additively, or with trade-offs), how costs change, how the total value is distributed across services, and how species overlap in their provisioning of multiple services.

Discussion

We derived the economically optimal biodiversity protection strategy that maximizes ecosystem service provision under uncertainty. Ecosystem services only provide an incentive for protecting all species in limited situations. When the species pool is large, some biodiversity loss creates little risk of losing services. Then, the costs of protection outweigh the expected benefits of protecting all species. Once the pool dwindles to a critical level, however, full protection becomes economically optimal. At this threshold, 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. We defined this threshold for several scenarios.

These results provide analytical insight into the degree to which conservation objectives can be achieved solely through efforts targeting ecosystem services. In the extreme, protecting all species is economically optimal when the ratio of value received from services to costs incurred by protection equals or exceeds β^* (*Fig. 3: Region 3*) **[2].** For all ratios of service value to protection costs below β^*, managing solely for ecosystem services will leave species at risk of functional extinction (*Fig. 3: Region 1*). This criterion defines the range of cases where an expanded toolbox of policies and management approaches (e.g., endangered species regulations, market-based incentives, etc.) will be required to protect biodiversity even in the presence of optimal management for ecosystem services. Several key implications for decision makers emerge.

The number of species critical to services influences conservation outcomes

The critical value-to-cost ratio that promotes 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; *SI*). 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 by estimating fractions of the species required to sustain one or more services through time (e.g., (11, 29, 48). 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 (49, 50). Across other systems, empirical studies suggest that the fraction of species directly involved in service provisioning can vary dramatically (*SI Table 1*). When such empirical estimates are available, our analytical results suggest how much greater the value of the service will need to be relative to the costs of species protection to warrant full biodiversity protection (Fig. 4, *SI Table 1*). Empirical estimates suggest the answer varies dramatically and predictably among services (Fig. 4; *SI Table 1*). In some cases a service value roughly equal to the costs of protection justifies full biodiversity protection, while in other cases the value of the service must exceed the cost 9 fold to justify full biodiversity protection (Fig. 4; *SI Table 1*). The ability to estimate this critical ratio makes it possible for decision makers to gain insight into when actions beyond promoting management for ecosystems services will be critical to biodiversity protection.

High costs dramatically reduce optimal protection levels

Increasing the costs of protecting species (either opportunity costs or direct costs of management) always decreases the anticipated amount of biodiversity protection afforded by management for ecosystems services (solutions **[1]** and **[3];** *Fig. S3*). Such costs can 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 palm oil (*Elaeis guineensis*) plantations and logging create relatively high opportunity costs (e.g., for Borneo, (51, 52). When opportunity costs grow, ecosystem services need to be even more valuable to incentivize protecting species. Zoning the land or ocean 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. Gains in efficiency that provide species protections at lower costs (e.g., identifying and eliminating threats more strategically – 54) could significantly enhance levels of biodiversity protection warranted by ecosystem services.

Payment for ecosystem services can enhance protection

Increasing the financial value of services relative to the costs incurred by conservation will always lead to higher levels of optimal biodiversity protection when there is uncertainty over how the services are produced (Fig. 3, **[1];** *Fig. S3*). One way to increase the service value is supplementing the market value for services with payment for ecosystem services (PES) programs. Solving for the optimal value-to-cost ratio, $\beta*$, can help define more rigorously what added service value a PES program must artificially create to promote sufficient protections for biodiversity. For instance, REDD+ aims to compensate landowners for maintaining tropical forests that sequester carbon. Since the current value of carbon credits is small relative to the opportunity costs from alternative uses such as logging or oil-palm plantations, studies predict that current PES programs are unable to compete (51, 52). Our model can help estimate how much higher payments need to be to foster full biodiversity protection.

Future directions

Although our theoretical analyses provide a framework for predicting when ecosystem services provide strong versus weak incentives for full biodiversity protection, they also raise several key questions that merit future research. First, scientific research can reduce uncertainties in managing for ecosystem services – including which species are critical for specific services and which species will be functionally lost without protection. What is the value of such new information? New science could identify which species are critical to protect for services, which thereby reduces the costs of maintaining the service. Although lower costs for biodiversity protection normally would enhance the optimal level of protection, better insight into which species are critical to protect to provide a service eliminates the incentive to protect non-critical species. Second, species interactions could alter how many or which species are required to maintain services. This model did not account for non-obligate species dependencies or the possibility of secondary extinctions following functional losses of species (54). Integrating species interactions into the framework may dramatically increase the number of species indirectly needed to secure services. Third, projects targeting ecosystem services could attract new sources of conservation funding rather than compete for existing resources (55); therefore, future work could more explicitly consider the role of budget constraints when quantifying the net effect on biodiversity of managing for ecosystem services rather than intrinsic value. Future research could explore these pressing questions.

Conclusions

Our theory suggests that managing ecosystems to maximize ecosystem services will commonly not benefit all biodiversity. Analytically, we quantify the conditions under which ecosystem services provide a sufficient economic incentive for protecting all species, when they justify protecting nothing, and cases in between. 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 beneficiaries value present versus future benefits (i.e., discounting), and **(4)** uncertainty over which species provide benefits. For instance, high opportunity costs will lower the level of biodiversity protection. In contrast, ecosystem service approaches will likely provide a greater incentive for biodiversity protection when there are multiple ecosystem services and when there is uncertainty about the species that are critical to providing the services.

Biodiversity can be critical to services. Nevertheless, a focus solely on ecosystem services may 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 sufficient economic incentives for 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.

Methods

The objective is to maximize the expected net present value of ecosystem services over an infinite horizon by investing in species protection now and in the future given uncertainty over the relationship between species and ecosystem service value (Fig. 1). To solve this problem generally, we formulate the decision process as a stochastic optimal control problem and solve it using stochastic dynamic programing (SDP) techniques ((43, 44) – 44 provides a primer for ecologists). SDP determines a management strategy (known as the optimal policy) that best achieves the decision-maker's objective over time, balancing current-period payoffs with future service value. Here, the optimal policy represents the sequence of actions (investment in protection or not at each species pool size) that maximizes the net ecosystem service value for an infinite time horizon.

In addition to defining an objective, stochastic optimal control problems require specifying: a set of actions, payoffs resulting from taking any particular action, an inter-temporal criterion to maximize, uncertainty, and the system's dynamics. With the following setup, we quantify how much biodiversity protection will arise solely from an effort to optimize ecosystem service value given uncertainty over the links between species and services:

- **State variables:** At the beginning of every period, the decision-maker observes the current size of the existing species pool (s_t) and whether or not the service is obtained. 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 (Fig. 1).

- **Actions:** The manager can choose to protect or not protect at a given sized species pool, s_t, after observing whether or not the service is obtained.
- **Dynamics:** When the manager does not protect the species pool, a random species will be lost in the next period, risking the loss of a critical species (from the subset k), and thus the reduction or full loss of the ecosystem service.
- **Immediate payoffs:** The current period payoff depends on whether the service is provided and what action is taken. We consider several functional relationships between the service payoff and the number of critical species: $f(s_t)$. In all cases, investing in protection incurs a cost c, whereas not protecting incurs no cost. The immediate payoff is the difference between these benefits and costs. For the simplest payoff function, if the service is provided, a benefit of v is obtained; if not, the benefit is 0. We also model cases where the payoff smoothly depends on the number of species providing it (r) following a linear, concave, or convex relationship. For this extension, we denote this payoff v_r where r indexes the number of species in the pool that can provide the service and is $\leq k$.
- **Inter-temporal value:** Optimizing the net value of the ecosystem service over time means maximizing the difference between service benefits (measured in dollars as revenues) and the costs required to achieve them. Future costs and

revenues are discounted by a factor δ according to standard cost-benefit analysis techniques from economics (42).

Based on this problem formulation, investing in species protection results in an immediate payoff of $f(s_t) - c$ (which is $v - c$ for the piecewise form and $v_r - c$ for the smooth form) plus a stream of 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 to the ecosystem service provision could be lost. The probability of retaining the service following the loss of a random species is $p(s_t,r) := \frac{s_t - r}{s_t}$ and depends on the size of the species pool and the number of critical species remaining (r out of the total k critical species). If the species pool is very large and the number of critical species is very small, the random loss of a species is unlikely to result in the loss of the service value. When the decision-maker chooses not to protect, the resulting payoff may be either v_r with probability $p(s_t,r)$ or v_{r-1} with the probability $1-p(s_t,r)$. For the piecewise case, payoffs will be either v with probability $p(s_t,k)$ or 0 (if a critical species is lost) with the probability $1-p(s_t,k)$. 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.

We use a combination of analytical and numerical approaches to find the level of biodiversity protection that maximizes the current and discounted future value from ecosystem services (detailed in *SI*). Fig. 2 illustrates the logic behind the primary Theorem, 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 state 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 $\bar{s}$, it is optimal not to protect; for species pools smaller than $\bar{s}$, it is optimal to protect (see *SI* for derivations of $\bar{s}$). We obtain a general, closed-form solution for this threshold $\bar{s}$, which characterizes the optimal policy – the level of biodiversity that maximizes net ecosystem service value over all periods given uncertainty (see **[1]**). To approximate the optimal policy when the level of the service depends linearly, concavely, or convexly on the number species providing the service, we use a standard *value iteration* numerical approach. The *Materials & Methods SI* describes the mathematical setup, theorems, analytical solutions (including for multiple services extension), and numerical analyses.

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Appendix for I. Supplemental Table

Table S1. The economic conditions required for full protection to be optimal given empirical estimates of the fraction of species directly critical to a particular service. Empirical estimates of this fraction vary across services and location, resulting in different β^* criteria -- the number of times greater the value needs to be than the cost for protecting everything to be optimal. This table also shows how society's preferences for the present versus the future will influence this outcome by comparing the economic criteria for two discount factors (0.95 and 0.99). In many cases, reviewing the literature yielded a range for the number of critical or total species, providing multiple estimates for fraction of critical species, therefore we present a range of the β^* criteria. The supplemental information provides more information on and references for each case study.

Service and location	**Estimated number of directly critical species (*k*)**	**Estimated total number of species in ecosystem (s_0)**	**β^* with discount factor of 0.95**	**β^* with discount factor of 0.99**	**References for estimates of *k* and s_0**
Wave attenuation, Carpentaria, California, U.S.A	**1-5**	**163** (includes parasites)	**2.58 - 9.1**	**1.32- 2.62**	Zedler *et al.* 2001; Hechinger *et al.* 2011
Pollination of watermelon crops, Yolo County, California,	**2*-30**	**1075- 2040**	**2.74-51.95**	**1.35-11.19**	Mayer & Laudenslayer 1989; Kremen *et al.* 2002

U.S.A.					
Pollination of watermelon crops, New Jersey & Pennsylvania, U.S.A.	**6-46****	**1338** (plants and animals)	**2.4-12.1**	**1.28- 3.22**	Winfree *et al.* 2007; New Jersey Pinelands Commission 2013
Carbon storage, Montes Azules Biosphere Reserve, Mexico	**22*****	**169** (tree species); **2171-5179** (plants and animals)	**1.33** (only trees); **5.88-12.72**	**1.07** (only trees); **1.98-3.4**	Balvanera *et al.* 2005; Parkswatch 2006
Carbon storage (mangroves), Deluge inlet/ Hinchinbrook channel, Australia	**4**	**71** (no parasites or planktons)	**1.84**	**1.17**	Clough 1998; Abrantes & Sheaves 2009
Carbon storage (mangroves), Sundarban, India	**30-36**	**1722**	**3.34-3.82**	**1.47-1.56**	Gopal & Chauhan 2006; Yao *et al.* 2011.

* As few as 2 bee species provided "ample" levels of pollination in 2001 in Kremen *et al.* (2002)

**6 species (of domesticated pollinators) may provide 91% of pollination of watermelon crops but up to 46 native species can provide this service (Winfree *et al.* 2007)

*** 22 tree species provide 90% of total carbon storage (Balvanera *et al*. 2005)

Appendix for I: "To what extent do ecosystem services motivate protecting biodiversity?"

1 Materials and Methods

The objective is to maximize net ecosystem service value over an infinite time horizon through investing in species protection given uncertainty over the relationship between species and ecosystem service value. To solve this problem generally, we formulate the decision process as a stochastic optimal control problem and solve it using stochastic dynamic programing (SDP) techniques (Marescot et al. [1] provides a primer on SDP for ecologist). SDP determines the management strategy (known as the optimal policy) that best achieves the decision-maker's objective over time, balancing current-period payoffs with future service value. The optimal policy induces a sequence of actions (investment in protection or not at each sized species pool) that maximizes the net ecosystem service value for an infinite time horizon.

We consider several model formulations as described in the main text and below. To introduce the theory, we first present the model setup and results where the current period payoff from an ecosystem services is v (if all of the k critical species remain in the species pool) or 0 following the functional loss of any of the critical species. We then present the model formulation, analyses, and results for the extension considering multiple ecosystem services. In section 3, we describe the model formulation and results for when the level of the service increases smoothly with the number of species providing it.

1.1 Mathematical problem statement

We consider a decision-maker managing a pool of species, among which some are critical to provide an ecosystem service. The manager does not have perfect information about which species are critical to the service. During a time period, one of the species will go functionally extinct, except if costly protection measures are taken. There is uncertainty over whether the species that will be functionally lost will be one that is critical to the service. In the paper, the manager's problem is formulated as a stochastic optimal control problem, with the following setup and variables.

Formalizing decision-making

Let $\mathbb{N}$ denote the set of non-negative integers $\mathbb{N} = \{0, 1, 2, \ldots\}$, and $\mathbb{N}^* = \{1, 2, \ldots\}$ the set of positive integers. Let the scalars $\upsilon > c > 0$ denote *ecosystem service payoff* (when all critical species are present in the pool) and *protection cost*, and let $0 < \delta < 1$ stand for a *discount factor*.

The *probability* $p_{kc}(s)$ *of losing one of the non-critical species* (*kc* for "keep critical") is a non-decreasing function $s \in \mathbb{N}^* \mapsto p_{kc}(s) \in [0, 1]$ of the size pool s, that is,

$$\underline{s} < \overline{s} \Rightarrow p_{kc}(\underline{s}) \leq p_{kc}(\overline{s}) \; . \tag{1}$$

We also consider the *probability* $p_{lc}(s)$*of losing one of the critical species* (*lc* for "lose critical")

$$p_{lc}(s) := 1 - p_{kc}(s) \; , \tag{2}$$

which is non-increasing with s. We suppose that the probability $p_{lc}(1)$ of losing a non-critical species when the pool is reduced to one single species is one:

$$p_{lc}(1) = 1 \ . \tag{3}$$

We consider a special case where $p_{kc}(s) = (s-k)_+/k$, when there are $k \geq 1$ critical species needed for the service (see §1.4).

Stochastic optimal control problem

At each time $t = 0, 1, \ldots$, running from 0 to $+\infty$, the decision-maker has to choose between two management options ($d \in \{\mathtt{P}, \mathtt{NP}\}$) for a pool of s species:

- Either she protects the pool ($d = \mathtt{P}$) at cost c and avoid the functional extinction of a random species. Therefore, she obtains the ecosystem service of value $\upsilon > c$ with certainty during the period $[t, t+1[$, hence the net value $\upsilon - c > 0$.
- Or she does not protect the pool ($d = \mathtt{NP}$). Not protecting will result in
  - either functionally losing a non-critical species with probability $p_{kc}(s)$ and obtaining the ecosystem service of value υ during the period $[t, t+1[$,
  - or functionally losing a critical species with probability $p_{lc}(s)$ and obtaining nothing.

Hence, the *mean current-period payoff* is

$$U(d, s) = \begin{cases} \upsilon - c & \text{if } d = \mathtt{P} \ , \\ p_{kc}(s)\upsilon & \text{if } d = \mathtt{NP} \ . \end{cases} \tag{4}$$

Letting $\delta \in (0,1)$ denote the discount factor, the manager maximizes the *mean intertemporal payoff*

$$\sum_{t=0}^{+\infty} \delta^t U(d_t, s_t) \; . \tag{5}$$

1.2 Bellman function and Bellman equation

We introduce the *Bellman function* J. By definition, $J(s)$ is the best intertemporal payoff

$$J(s) = \max_{(d_t)_{t=0,\dots,+\infty}} \sum_{t=0}^{+\infty} \delta^t U(d_t, s_t) \; , \tag{6a}$$

achieved over all possible streams $(d_t)_{t=0,\dots,+\infty}$ of decisions $d_t \in \{\mathtt{P}, \mathtt{NP}\}$, where the number s_t of species in the pool at time t starts with $s_0 = s$ species at time $t = 0$, and then follows the dynamics

$$s_0 = s \text{ and } s_{t+1} = \begin{cases} s_t & \text{if } d_t = \mathtt{P} \; , \\ s_t - 1 & \text{if } d_t = \mathtt{NP} \; . \end{cases} \tag{6b}$$

The above equations express that the number of species does not change if protection measures are taken, but drops by one unit (here, a species) if protection measures are not taken.

Proposition 1. *The Bellman function J is solution to the* Bellman equation

$$J(s) = \max\{v - c + \delta J(s); p_{kc}(s)[v + \delta J(s-1)]\} \; , \; \forall s = 1, 2, \dots \tag{7a}$$

$$J(0) = 0 \tag{7b}$$

Proof. Indeed, we have

$$
\begin{aligned}
J(s) &= \max_{(d_t)_{t=0,\dots,+\infty}} \sum_{t=0}^{+\infty} \delta^t U(d_t, s_t) \text{ by (6a)} , \\
&= \max_{d_0 \in \{\mathtt{P},\mathtt{NP}\}} \max_{(d_t)_{t=1,\dots,+\infty}} \sum_{t=0}^{+\infty} \delta^t U(d_t, s_t) , \\
&= \max_{d_0 \in \{\mathtt{P},\mathtt{NP}\}} \left(U(d_0, s) + \delta \max_{(d_t)_{t=1,\dots,+\infty}} \sum_{t=1}^{+\infty} \delta^{t-1} U(d_t, s_t) \right) , \\
&= \max \left\{ U(\mathtt{P}, s) + \delta \max_{s_1=s,(d_t)_{t=1,\dots,+\infty}} \sum_{t=1}^{+\infty} \delta^{t-1} U(d_t, s_t), \right. \\
&\qquad \left. U(\mathtt{NP}, s) + \delta \max_{s_1=s-1,(d_t)_{t=1,\dots,+\infty}} \sum_{t=1}^{+\infty} \delta^{t-1} U(d_t, s_t) \right\}
\end{aligned}
$$

because

- either the manager protects the pool ($d_0 = \mathtt{P}$), obtains $U(\mathtt{P}, s)$ and the pool size remains at s,
- or she does not ($d_0 = \mathtt{NP}$), obtains $U(\mathtt{NP}, s)$ and the pool size goes down to $s - 1$.

Therefore, going on, we obtain

$$
\begin{aligned}
J(s) &= \max \{ U(\mathtt{P}, s) + \delta J(s), U(\mathtt{NP}, s) + \delta J(s-1) \} \text{ by (6a)} , \\
&= \max \{ v - c + \delta J(s), p_{kc}(s) v + \delta J(s-1) \} \text{ by (4)} .
\end{aligned}
$$

This ends the proof. □

The Bellman equation (7) yields an *optimal policy* $\pi^\star : \mathbb{N} \to \{\mathtt{P}, \mathtt{NP}\}$, such that $d_t = \pi^\star(s_t)$ maximizes (5), where s_t is given by (6b).

1.3 Analysis of the Bellman equation

The mathematical results of this paper revolve around the analysis of the Bellman equation. We start with the Bellman equation (also known as a dynamic programming equation) in an implicit form, as the solution $J(s)$ appears on both sides of the equality (7a).

We provide an explicit solution to the Bellman equation (7) in two steps. First, we turn the implicit Bellman equation (7) into an explicit form. Second, we characterize the Bellman function (6) as a piecewise function with a switching point (*a threshold number of species*) between two regimes for the optimal policy. This threshold number of species characterizes the level of biodiversity protection that maximizes ecosystem service value over an infinite time horizon. We therefore call this number of species the "optimal level of protection." In relevant cases, we obtain a closed form solution for this threshold number of species, and we are able to characterize the optimal level of protection as a function of the model's parameters. The following proofs draw on two technical Lemmas, which are included in the Appendix.

1.3.1 Turning the implicit Bellman equation into an explicit form

Using Lemma 1, we can convert (7a) from an implicit form into an equality where $J(s)$ appears on one side and $J(s-1)$ on the other side. We use the following notation for the payoff that results from *protecting all of the time*:

$$\vartheta = \sum_{t=0}^{+\infty} \delta^t (\upsilon - c) = \frac{\upsilon - c}{1 - \delta} > 0 \; . \tag{8}$$

Proposition 2. *The Bellman equation* (7) *is equivalent to*

$$J(s) = \max\{\vartheta; p_{kc}(s)[v + \delta J(s-1)]\} \ , \ \ \forall s \in \mathbb{N}^* \ , \tag{9a}$$

$$J(0) = 0 \ . \tag{9b}$$

The Bellman function $J(s)$ is non-decreasing in s.

Proof. First, we prove that (7) is equivalent to (9). For this purpose, we apply Lemma 1 with $\mathbb{X} = \mathbb{R}$ and $f(x) = v - c + \delta x$. Its two assumptions are satisfied:

1. f has a (unique) fixed point $\overline{a} = \frac{v-c}{1-\delta} = \vartheta$, given by (8);
2. $x \mapsto f(x) - x = v - c - (1-\delta)x$ is decreasing, since $1 - \delta > 0$.

We rewrite equation (7a) as $a = \max\{f(a), b\}$ with

- $a = J(s)$,
- $f(a) = v - c + \delta J(s)$,
- $b = p_{kc}(s)[v + \delta J(s-1)]$.

By (56), $a = \max\{f(a), b\} \iff a = \max\{\overline{a}, b\}$, and therefore:

$$\text{(7a)} \iff J(s) = \max\{\vartheta; p_{kc}(s)[v + \delta J(s-1)]\} \ . \tag{10}$$

Now, we can prove that the Bellman function $J(s)$ is non-decreasing in s. For this purpose, we prove by induction that $J(s) \geq J(s-1)$ for all $s \in \mathbb{N}^*$. By (9), we have

$$J(1) = \max\{\vartheta; p_{kc}(1)v\} \geq 0 = J(0) \ .$$

Suppose now that $J(s-1) \geq J(s-2)$. We deduce that

$$\begin{aligned}
J(s) &= \max\left\{\vartheta; p_{kc}(s)[v + \delta J(s-1)]\right\} \text{ by (9) ,} \\
&\geq \max\left\{\vartheta; p_{kc}(s-1)[v + \delta J(s-1)]\right\} \text{ since } p_{kc}(s) \geq p_{kc}(s-1) \text{ by (1),} \\
&\geq \max\left\{\vartheta; p_{kc}(s-1)[v + \delta J(s-2)]\right\} \text{ since } J(s-1) \geq J(s-2) \text{ ,} \\
&= J(s-1) \text{ by (9).}
\end{aligned}$$

This ends the proof. □

1.3.2 Characterizing two management regimes for the optimal policy

We now characterize the Bellman function J as a piecewise function with a switching point[1] between two management regimes for the optimal policy.

We find that, when the size of the species pool s falls below a critical size, denoted $\bar{s}$, the optimal strategy is to protect the remaining species. At $s \leq \bar{s}$, the risk of losing the service exceeds a *pivotal probability*, which we define as

$$\bar{p}_{lc} := \frac{c - \delta c}{v - \delta c} \ . \tag{11}$$

This pivotal probability $\bar{p}_{lc}$ and the threshold number $\bar{s}$ of species are related by

$$s \leq \underbrace{\bar{s}}_{\text{threshold number of species}} \iff \underbrace{p_{lc}(s)}_{\substack{\text{probability of losing} \\ \text{a critical species}}} \geq \underbrace{\bar{p}_{lc}}_{\text{pivotal probability}} \ . \tag{12}$$

Thus, when the number s of species falls below the threshold number $\bar{s}$ of species, the probability $p_{lc}(s)$ of losing a critical species rises above the pivotal probability $\bar{p}_{lc}$, making

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[1] The quantity $\bar{s}$ in (58) deserves the name of "switching point" only when $\bar{s} < +\infty$ because, else, there is a single regime.

protection the optimal management strategy.

We define the threshold number of species — the optimal number of species to protect — as

$$\overline{s} := \min\{s = 1, 2, 3, \dots \mid p_{lc}(s) \leq \bar{p}_{lc}\} \ , \tag{13}$$

with the convention that $\min \emptyset = +\infty$. We have that $\overline{s} > 1$, by the assumption (3) that the probability $p_{lc}(1)$ a losing one of the critical species when the pool is reduced to a single species is one. Indeed, $p_{lc}(1) = 1 > \bar{p}_{lc}$ implies that $\overline{s} > 1$ in (16). When $\overline{s} < +\infty$, the threshold number $\overline{s}$ of species is characterized by

$$p_{lc}(\overline{s} - 1) < \bar{p}_{lc} \leq p_{lc}(\overline{s}) \ . \tag{14}$$

Conversely, the probability of having the service following the loss of an additional species is

$$\bar{p}_{kc} := 1 - \bar{p}_{lc} = \frac{\upsilon - c}{\upsilon - \delta c} \ . \tag{15}$$

Therefore, the threshold number $\overline{s}$ can also be defined in terms of the probability $p_{kc}(s)$ of having the service, that is,

$$\overline{s} = \min\{s = 2, 3, \dots \mid p_{kc}(s) \geq \frac{\upsilon - c}{\upsilon - \delta c}\} \ , \tag{16}$$

with the convention that $\min \emptyset = +\infty$.

Theorem 1. *The Bellman function J in* (6) *is given by*[2] *the following induction*

$$J(s) = p_{kc}(s)[\upsilon + \delta J(s-1)] \,, \qquad \forall s = \overline{s}, \overline{s}+1, \dots \,, \tag{17a}$$

$$J(s) = \vartheta \,, \qquad \forall s = 1, \dots, \overline{s}-1 \,, \tag{17b}$$

$$J(0) = 0 \,. \tag{17c}$$

The optimal policy $\pi^\star : \mathbb{N} \to \{\mathrm{P}, \mathrm{NP}\}$ *displays two regimes:*

- *when the species pool is small, i.e. when* $s \leq \overline{s} - 1$*, it is optimal to protect it;*
- *when the species pool is large, i.e. when* $s \geq \overline{s}$*, it is optimal not to protect it.*

1.3.3 Characterizing optimal management trajectories

Before presenting the proof, we discuss the results to provide intuition about the optimal management trajectories.

Optimal trajectories

- The case $\overline{s} = +\infty$ corresponds to a high probability of losing a critical species, no matter how large the species pool is. Indeed, by (16), we have that

  $$\overline{s} = +\infty \iff p_{lc}(s) > \bar{p}_{lc} \,, \ \forall s \in \mathbb{N}^* \,. \tag{18}$$

  In that case, it is always optimal to protect regardless of the number s of species.

- By contrast, when $\overline{s} < +\infty$, it is only optimal to protect when the probability of losing a critical species (and therefore the service) strictly exceeds the pivotal probability $\bar{p}_{lc}$. Therefore,

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[2] When $\overline{s} = +\infty$, (17a) is meaningless and (17b) is to be understood $\forall s \in \mathbb{N}^*$.

- if the initial species pool s_0 is small enough that $s_0 \leq \overline{s} - 1$, the probability of losing a critical species strictly exceeds the pivotal probability $\bar{p}_{lc}$; as a result, it is always optimal to protect the pool;
- if the initial species pool s_0 is large, such that $s_0 \geq \overline{s}$, it is optimal not to protect and functionally lose species until the size of the species pool reaches $\overline{s} - 1$, at which point it is optimal to protect the remaining species forever.

1.3.4 The myopic decision-maker protects less than a foresighted one

We compare optimal and myopic policies. A myopic policy is one where a manager only maximizes value from the current period with no regard for the future (i.e., with a discount factor $\delta = 0$). The *myopic manager* maximizes the mean current period payoff (4), solving

$$\max_{d \in \{\texttt{P},\texttt{NP}\}} U(d, s) = \max\{\upsilon - c, p_{kc}(s)\upsilon\} = \max\{-c, -p_{lc}(s)\upsilon\} + \upsilon \ . \tag{19}$$

We see that the optimal policy of the myopic decision-maker is not to protect when $s \geq \underline{s}$, and to protect when $s \leq \underline{s} - 1$, where

$$\underline{s} := \min\{s = 1, 2, 3, \dots \mid p_{lc}(s) \leq \frac{c}{\upsilon}\} \tag{20}$$

is the *myopic critical number of species*.

Now, we can easily prove that $\bar{p}_{lc} < c/\upsilon$ because $c > 0$. As $p_{lc}(s)$ goes down as s increases, it first crosses $\underline{s}$ at c/υ, then $\overline{s}$ at $\bar{p}_{lc}$. Hence, comparing (20) with (16), we deduce that

$$\underline{s} \leq \overline{s} \ . \tag{21}$$

In other words, compared with the foresighted manager, *the myopic manager protects less* because his threshold for triggering protection is lower.

1.3.5 Proof of Theorem 1

Proof. We use Lemma 2 with $\mathbb{S} = \mathbb{N}^*$ and

- $A(s) = J(s)$,
- $B(s) = p_{kc}(s)[\upsilon + \delta J(s-1)]$,
- $C(s) = \vartheta$.

Lemma 2 can be applied because its assumption is satisfied:

$$s \mapsto B(s) - C(s) = p_{kc}(s)[\upsilon + \delta J(s-1)] - \vartheta$$

is non-decreasing. Indeed, the term $p_{kc}(s)[\upsilon + \delta J(s-1)]$ is non-decreasing in s as $p_{kc}(s)$ and $J(s-1)$ are non-decreasing non-negative functions of s (see Proposition 2), and their product is therefore a non-decreasing function.

We define $\overline{\overline{s}}$ as in (58) by

$$\overline{\overline{s}} = \min\{s = 1, 2, \dots \mid p_{kc}(s)[\upsilon + \delta J(s-1)] \geq \vartheta\} \ , \tag{22}$$

with the convention that $\min \emptyset = +\infty$.

Equation (9a) is $A(s) = \max\{B(s), C(s)\}$. From the equivalence (59), we obtain that[3]

$$J(s) = p_{kc}(s)[\upsilon + \delta J(s-1)] \ , \qquad \forall s = \overline{\overline{s}}, \overline{\overline{s}}+1, \dots \ , \tag{23a}$$

$$J(s) = \vartheta \ , \qquad \forall s = 1, \dots, \overline{\overline{s}}-1 \ , \tag{23b}$$

$$J(0) = 0 \ . \tag{23c}$$

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[3] When $\overline{\overline{s}} = +\infty$, (23a) is meaningless and (23b) is to be understood $\forall s \in \mathbb{N}^*$.

Therefore, comparing (23) with (17), it is enough to show that $\overline{\overline{s}} = \overline{s}$ to complete the proof.

First, we prove that $\overline{\overline{s}} \geq \overline{s}$. When $\overline{\overline{s}} = +\infty$, this inequality is clear. We consider two other cases.

The first case assumes that $2 \leq \overline{\overline{s}} < +\infty$. By (22), we have that $p_{kc}(\overline{\overline{s}})[\upsilon + \delta J(\overline{\overline{s}} - 1)] \geq \vartheta$. By (23b), we have that $J(\overline{\overline{s}} - 1) = \vartheta$. From these relationships, we deduce that $p_{kc}(\overline{\overline{s}})[\upsilon + \delta\vartheta] \geq \vartheta$, and therefore that $p_{kc}(\overline{\overline{s}}) \geq \frac{\vartheta}{\upsilon+\delta\vartheta} = \frac{\upsilon-c}{\upsilon-\delta c}$. This gives $p_{lc}(\overline{\overline{s}}) = 1 - p_{kc}(\overline{\overline{s}}) \leq \frac{c-\delta c}{\upsilon-\delta c} = \bar{p}_{lc}$ by (11). By definition (16) of $\overline{s}$, we conclude that $\overline{\overline{s}} \geq \overline{s}$.

The second case is when $\overline{\overline{s}} = 1$, but we show that this case is empty. Indeed, in this case, $J(\overline{\overline{s}} - 1) = J(0) = 0$ by (23c). By (22), we deduce that $J(\overline{\overline{s}}) = p_{kc}(1) \geq \vartheta/\upsilon$. However, this inequality cannot hold because $p_{kc}(1) = 0$ by (3).

Second, we prove that $\overline{s} \geq \overline{\overline{s}}$. This inequality is obvious when $\overline{s} = +\infty$. Again, we consider two cases parallel to those above.

The first case assumes that $2 \leq \overline{s} < +\infty$. From (23a) and (23b), we obtain that $J(s) \geq \vartheta$, for all $s \geq 1$, because $J(s)$ is non-decreasing in s (see Proposition 2). Since $2 \leq \overline{s} < +\infty$, $\overline{s}$ satisfies $p_{kc}(\overline{s}) \geq \frac{\upsilon-c}{\upsilon-\delta c}$ by (14). From those two inequalities, we deduce that

$$p_{kc}(\overline{s})[\upsilon + \delta J(\overline{s} - 1)] \geq \frac{\upsilon - c}{\upsilon - \delta c}[\upsilon + \delta\vartheta] = \frac{\vartheta}{\upsilon + \delta\vartheta}[\upsilon + \delta\vartheta] = \vartheta \ ,$$

by (8). Therefore, from (22), we conclude that $\overline{s} \geq \overline{\overline{s}}$.

The second case occurs when $\overline{s} = 1$, but this is an empty case as we have seen that $\overline{s} > 1$.

To sum up, considering all cases, we have shown that $\overline{\overline{s}} = \overline{s}$. Together with (23), we conclude that (17) holds true. The optimal policy follows and the proof is complete. □

1.4 Optimal protection level when k critical but unknown species provide a service

Here, we still suppose that we do not know which species are critical, but we assume that we know the size $k \in \mathbb{N}^*$ of the subset of critical species, as described in the main text. When a pool of s species is not protected, the probability of having the service after the functional loss of a species is the probability of losing one of the $s - k$ non-critical species: $p_{kc}(s) = (s - k)_+/k$, that is,

$$p_{kc}(s) = 0 \ , \ \ \forall s = 1, \ldots, k \quad \text{and} \quad p_{kc}(s) = \frac{s - k}{s} \ , \ \ \forall s = k + 1, \ldots s_0 \ . \tag{24}$$

We provide an explicit, closed-form expression for the critical number of species to protect $\overline{s}$ in (16). This allows us to analyze how the optimal level of species protection varies with the parameters of the problem, in particular with *ratio of value to costs*

$$\beta = \frac{v}{c} \ . \tag{25}$$

Proposition 3. *When the probability $p_{kc}(s)$ is given by* (24)*, the critical species pool size $\overline{s}$ in* (16) *is the unique integer $\overline{s} \geq k + 1$ such that*

$$\overline{s} \geq \frac{k}{\bar{p}_{lc}} > \overline{s} - 1 \ . \tag{26}$$

In other words, $\overline{s} = \lceil k/\bar{p}_{lc} \rceil$, the ceiling integer *of $k/\bar{p}_{lc}$. Equivalently, $\overline{s}$ can be rewritten in terms of the ratio β of value to costs in* (25)*:*

$$\bar{s} \geq \frac{k(\beta - \delta)}{1 - \delta} > \bar{s} - 1 \ . \tag{27}$$

Proof. By (24), $p_{kc}(1) = \cdots = p_{kc}(k) = 0$. Therefore, we deduce from (16) that

$$\overline{s} = \min\{s = k+1, \dots \mid \frac{s-k}{s} \geq \frac{\upsilon - c}{\upsilon - \delta c}\} \ .$$

Thanks to the expression (11) of $\bar{p}_{lc}$, and by easy algebraic rearranging, inequalities (26) and (27) follow. □

By (12) and Theorem 1, protection is optimal for a pool of size s if and only if $s \leq \bar{p}_{lc} k - 1$. The pivotal pool size $\overline{s}$ is approximately proportional to the number k of critical species, with $1/\bar{p}_{lc}$ as a multiplier.

- If $\upsilon \approx c$, then $\bar{p}_{lc} \approx 1$ and $\overline{s} \approx k$
- If $\upsilon >> c$, then $\bar{p}_{lc} \approx 0$ and $\overline{s}$ is very large.

Proposition 4. *When the probability $p_{kc}(s)$ is given by* (24)*, protecting all the $s_0 > k$ species present is always optimal when*

$$\beta = \frac{\upsilon}{c} \geq \beta^*(s) = \delta + (1-\delta)\frac{s}{k} \ . \tag{28}$$

Notice that the right hand side $\beta^*(s)$ of (28) is a convex combination of 1 and s/k:

- if $\delta \approx 0$ — that is, if there is no preference for the future (relative to the present) — then you require a high ratio of value to costs $\beta^*(s) \approx s/k$ to protect; it will be even larger for larger species pools s;
- if $\delta \approx 1$ — that is, if the future is weighted equally with the present — then you require a ratio of value to costs $\beta^*(s) \approx 1$ to protect all species.

1.5 The case of multiple ecosystem services: are optimal protection levels higher?

Now, we analyze the Bellman equation for two ecosystem services. Let $(i, j) \in \{0, 1\}^2$ represent both services together ($i = j = 1$), only one of the services ($i \neq j$), or no services at all ($i = j = 0$). Thus, with notations from the previous sections, we will model a series of ecosystem values υ_{ij}, with probability functions p_{ij} and Bellman functions J_{ij}. All results below can be extended to more than two ecosystem services.

1.5.1 Bellman function and Bellman equation for multiple services

Considering the case of two services, the Bellman function for services $(i, j) \in \{0, 1\}^2$ is denoted by J_{ij}. For consistency of notations, we set

$$\upsilon_{00} = 0 \ , \ \ p_{00}(s) = 0 \ , \ \ J_{00}(s) = 0 \ , \tag{29a}$$

so that the following kind of identities will hold true:

$$\sum_{i,j} [\cdot]_{ij} = \sum_{(i,j)\in\{0,1\}^2} [\cdot]_{ij} = \sum_{(i,j)\in\{0,1\}^2,(i,j)\neq(0,0)} [\cdot]_{ij} = [\cdot]_{11} + [\cdot]_{10} + [\cdot]_{01} \ , \tag{29b}$$

and

$$\sum_{i\neq j} [\cdot]_{ij} = \sum_{(i,j)\in\{0,1\}^2,i\neq j} [\cdot]_{ij} = [\cdot]_{10} + [\cdot]_{01} \ . \tag{29c}$$

The Bellman equation for J_{11} is

$$J_{11}(s) = \max\{\upsilon_{11} - c + \delta J_{11}(s); \sum_{(i,j)\in\{0,1\}^2} p_{ij}(s)[\upsilon_{ij} + \delta J_{ij}(s-1)]\} \ , \tag{30}$$

for all $s \in \mathbb{N}^*$, and $J_{11}(0) = 0$. In the above expression, the Bellman functions J_{01} and J_{10} have been studied in §1.3 and are given by Theorem 1. We set

$$\vartheta_{ij} = \frac{\upsilon_{ij} - c}{1-\delta} > 0 \; . \tag{31}$$

Proposition 5. *The Bellman function* $J_{11}(s)$ *is non-decreasing in* s*. The Bellman equation* (30) *is equivalent to*

$$J_{11}(s) = \max\{\vartheta_{ij}; \sum_{(i,j)\in\{0,1\}^2} p_{ij}(s)[\upsilon_{ij} + \delta J_{ij}(s-1)]\} \; , \tag{32}$$

for all $s \in \mathbb{N}^*$*, and* $J_{11}(0) = 0$*. As a consequence,* (30) *has a unique solution.*

Proof. The Bellman function $J_{11}(s)$ is non-decreasing in s, by the same argument as in the proof of Proposition 2.

For the rest, we apply Lemma 1 with $\mathbb{X} = \mathbb{R}$ and $f(x) = \upsilon_{11} - c + \delta x$. Its two assumptions are satisfied:

1. f has a (unique) fixed point $\overline{a} = \frac{\upsilon_{11}-c}{1-\delta} = \vartheta_{11}$, given by (8);
2. $x \mapsto f(x) - x = \upsilon_{11} - c - (1-\delta)x$ is decreasing, since $1 - \delta > 0$.

We rewrite equation (30) as $a = \max\{f(a), b\}$ with

- $a = J_{11}(s)$
- $f(a) = \upsilon_{11} - c + \delta J_{11}(s)$,
- $b = \sum_{(i,j)\in\{0,1\}^2} p_{ij}(s)[\upsilon_{ij} + \delta J_{ij}(s-1)]$.

By (56), $a = \max\{f(a), b\} \iff a = \max\{\overline{a}, b\}$, and therefore (30) is equivalent to (32). □

The following result is less powerful than Theorem 1, because the threshold number of species that is optimal to protect for multiple services, $\overline{s}_{11}$, is not characterized in terms of the parameters, but depends on the solution J_{11}.

Proposition 6. *Let*

$$\overline{s}_{11} = \min\{s = 1, 2, \dots \mid \sum_{(i,j)\in\{0,1\}^2} p_{ij}(s)[\upsilon_{ij} + \delta J_{ij}(s-1)] \geq \vartheta_{11}\} \, , \tag{33}$$

with the convention that $\min\emptyset = +\infty$*. The solution* J_{11} *to* (30) *is given by*[4] *the following induction*

$$J_{11}(s) = \sum_{(i,j)\in\{0,1\}^2} p_{ij}(s)[\upsilon_{ij} + \delta J_{ij}(s-1)] \, , \qquad \forall s = \overline{s}_{11}, \dots \, , \tag{34a}$$

$$J_{11}(s) = \vartheta_{11} \, , \qquad \forall s = 1, \dots, \overline{s}_{11} - 1 \, , \tag{34b}$$

$$J_{11}(0) = 0 \, . \tag{34c}$$

The optimal policy $\pi^\star : \mathbb{N} \to \{\mathit{P}, \mathit{NP}\}$ *displays two management strategy regimes:*

- *when the species pool is small, specifically when* $s \leq \overline{s}_{11} - 1$*, it is optimal to protect it;*
- *when the species pool is large, specifically when* $s \geq \overline{s}_{11}$*, it is optimal not to protect it.*

Proof. We use Lemma 2 with $\mathbb{S} = \mathbb{N}^*$ and

- $A(s) = J_{11}(s)$,
- $B(s) = \sum_{(i,j)\in\{0,1\}^2} p_{ij}(s)[\upsilon_{ij} + \delta J_{ij}(s-1)]$,

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[4] When $\overline{s}_{11} = +\infty$, (34a) is biologically meaningless and (34b) is to be understood $\forall s = 1, 2, \dots$

- $C(s) = \vartheta_{11}$.

Lemma 2 can be applied because its assumption is satisfied:

$$s \mapsto B(s) - C(s) = \sum_{(i,j) \in \{0,1\}^2} p_{ij}(s)[v_{ij} + \delta J_{ij}(s-1)] - \vartheta_{11}$$

is non-decreasing. Indeed, for all i, j, the term $p_{ij}(s)[v + \delta J_{ij}(s-1)]$ is non-decreasing in s as $p_{ij}(s)$ and $J_{ij}(s-1)$ are non-decreasing non-negative functions of s (see Propositions 2 and 5), and their product is therefore a non-decreasing function.

We define $\overline{s}_{11}$ as in (58) by (33). Equation (32) is $A(s) = \max\{B(s), C(s)\}$. From the equivalence (59), we obtain (34). $\square$

1.5.2 Case where different subsets of species are required for different services

We present the problem formulation for which a union of subsets of species is needed for two services. Again, the manager knows the size of the subsets of critical species but not which species are needed to obtain the service in all periods.

Let k_{10}, k_{01} and k_{11} be positive integers such that

$$p_{10}(s) = \frac{(s-k_{10})_+}{s}\ ,\ \ p_{01}(s) = \frac{(s-k_{01})_+}{s}\ ,\ \ p_{11}(s) = \frac{(s-k_{11})_+}{s}\ . \tag{35}$$

Fig S1 is a special case where $k_{11} = k_{01} + k_{10}$.

Proposition 7. *If two services*

1. *require a critical number k_{11} of species larger than what is required for each service, that is,*

$$k_{11} \geq \max\{k_{10}, k_{01}\}\ , \tag{36}$$

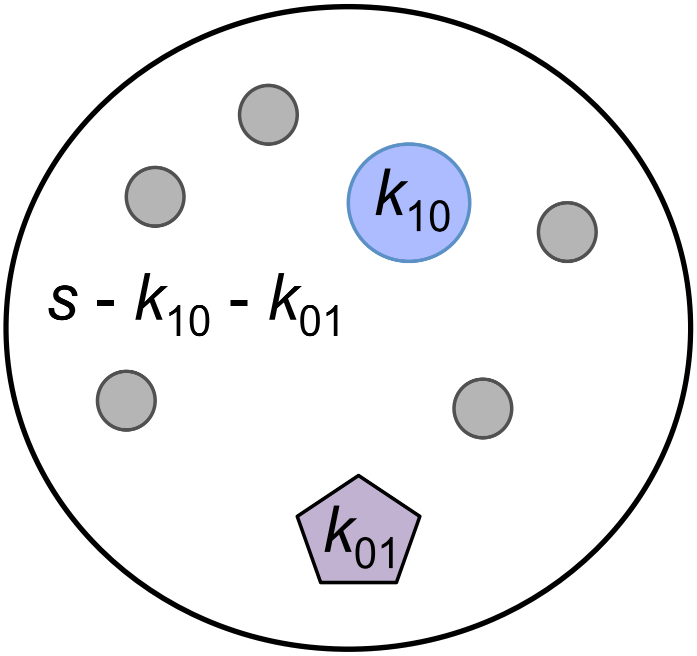

Figure S1: A pool of species that produces two services. Each service ij is delivered by non-overlapping subsets of critical species: k_{10} and k_{01}. The remaining $s - k_{10} - k_{01}$ species do not contribute to either service.

2. *are such that the value produced from multiple services is greater than or equal to the value of the best single service, that is,*

$$\upsilon_{11} \geq \max\{\upsilon_{10}, \upsilon_{01}\} \ , \tag{37}$$

then the size pool $\overline{s}_{11}$ *below which protecting is optimal in presence of two services satisfies*

$$\overline{s}_{11} \geq \max\{\overline{s}_{10}, \overline{s}_{01}\} \ . \tag{38}$$

These statements and proofs can easily be extended to more than two services.

Statements 1 and 2 both have a clear empirical interpretation. First, K_{10} is the subset of species that deliver service 1, where K_{01} is the subset that delivers service 2 and K_{11} is the subset that delivers both services. If both groups of species are needed to deliver both services, this scenario translates into

$$K_{11} \supset K_{10} \cup K_{01} \ . \tag{39}$$

Here, k_{10}, k_{01} and k_{11} are the respective numbers of species within these subsets (i.e., the cardinal of these sets K_{01},K_{10}, and K_{11}). Then, statement 1 follows from

$$K_{11} \supset K_{10} \cup K_{01} \Rightarrow k_{11} \geq \max\{k_{10}, k_{01}\} \ . \tag{40}$$

The second statement means that the value produced by multiple services is greater than or equal to the largest single service. So, suppose that $\upsilon_{10} = \varphi(K_{10})$, $\upsilon_{01} = \varphi(K_{01})$ and $\upsilon_{11} = \varphi(K_{11})$, where φ is a non-decreasing function (from sets to values). Then, statement 2 follows from

$$K_{11} \supset K_{10} \cup K_{01} \Rightarrow \upsilon_{11} = \varphi(K_{11}) \geq \max\{\varphi(K_{10}), \varphi(K_{01})\} = \max\{\upsilon_{10}, \upsilon_{01}\} \ . \tag{41}$$

Proof. Following (11), we define

$$\bar{p}_{10} = \frac{c - \delta c}{\upsilon_{10} - \delta c} \ , \ \ \bar{p}_{01} = \frac{c - \delta c}{\upsilon_{01} - \delta c} \ , \ \ \bar{p}_{11} = \frac{c - \delta c}{\upsilon_{11} - \delta c} \ .$$

We have the inequalities

$$\begin{aligned} \frac{1}{\bar{p}_{11}} &= \frac{\upsilon_{11} - \delta c}{c - \delta c} \\ &\geq \frac{\max\{\upsilon_{10}, \upsilon_{01}\} - \delta c}{c - \delta c} \text{ since } \upsilon_{11} \geq \max\{\upsilon_{10}, \upsilon_{01}\} \\ &= \max\{\frac{\upsilon_{10} - \delta c}{c - \delta c}, \frac{\upsilon_{01} - \delta c}{c - \delta c}\} \\ &= \max\{\frac{1}{\bar{p}_{10}}, \frac{1}{\bar{p}_{01}}\} \ . \end{aligned}$$

We deduce that

$$\begin{aligned} \frac{k_{11}}{\bar{p}_{11}} &\geq \max\{\frac{k_{11}}{\bar{p}_{10}}, \frac{k_{11}}{\bar{p}_{01}}\} \\ &\geq \max\{\frac{\max\{k_{10}, k_{01}\}}{\bar{p}_{10}}, \frac{\max\{k_{10}, k_{01}\}}{\bar{p}_{01}}\} \text{ since } k_{11} \geq \max\{k_{10}, k_{01}\} \\ &\geq \max\{\frac{k_{10}}{\bar{p}_{10}}, \frac{k_{01}}{\bar{p}_{01}}\} \ . \end{aligned}$$

By (3), we have

$$\bar{s}_{10} = \lceil k_{10}/\bar{p}_{10} \rceil \ , \ \ \bar{s}_{01} = \lceil k_{01}/\bar{p}_{01} \rceil \ , \ \ \bar{s}_{11} = \lceil k_{11}/\bar{p}_{11} \rceil \ .$$

Since the ceiling integer function $\lceil \quad \rceil$ is non-decreasing, we conclude that

$$\overline{s}_{11} = \lceil \frac{k_{11}}{\bar{p}_{11}} \rceil \geq \lceil \max\{\frac{k_{10}}{\bar{p}_{10}}, \frac{k_{01}}{\bar{p}_{01}}\} \rceil = \max\{\lceil \frac{k_{10}}{\bar{p}_{10}} \rceil, \lceil \frac{k_{01}}{\bar{p}_{01}} \rceil\} = \max\{\overline{s}_{10}, \overline{s}_{01}\} \ .$$

This ends the proof. □

2 Supporting results: how does the optimal level of protection depend on each variable?

We can address how the optimal level of biodiversity protection from (27) changes with shifts in the value of the service, costs associated with protective action, discount factor (δ), and number of species presumed to be critical to the service (k).

First, the optimal level of protection, $\overline{s}$, depends linearly on the number of species critical to the service (k) (Fig S2).

$$\frac{\partial \overline{s}}{\partial k} = \frac{\beta - \delta}{1 - \delta} \tag{42}$$

Second, increasing v, the current period payoff from the service, also increases the optimal protection level linearly (Fig S3):

$$\frac{\partial \overline{s}}{\partial v} = \frac{k\frac{1}{c}(1-\delta)}{(1-\delta)^2} = \frac{\frac{k}{c}}{1-\delta} \tag{43}$$

The degree to which increasing v will increase $\overline{s}$ will therefore depend on the values for k, c, and δ.

Third, cutting the costs incurred by protective action (including direct management costs and opportunity costs) can dramatically increase the optimal protection levels. On

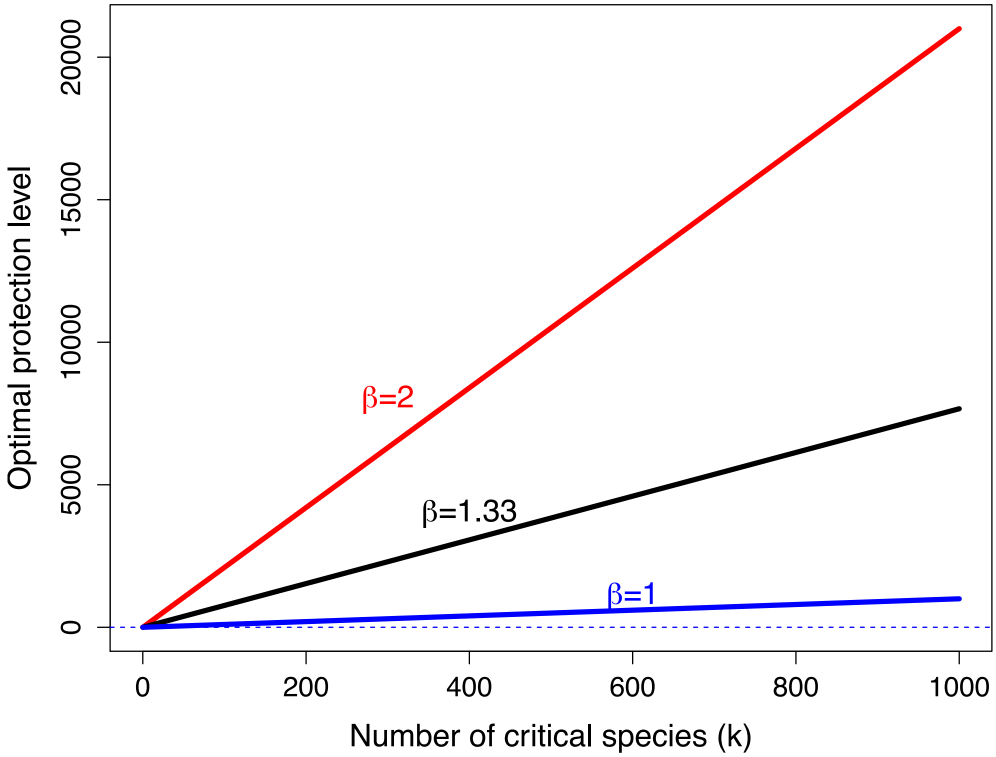

Figure S2: The optimal level of protection, $\overline{s}$, depends linearly on the number of critical species providing the service (k). This relationship is shown for different value-to-cost ratios (β) and for $\delta = 0.95$.

the other hand, small increases in c can dramatically (non-linearly) reduce $\overline{s}$:

$$\frac{\partial \overline{s}}{\partial c} = -\frac{kv}{c^2(1-\delta)} \tag{44}$$

Note that a small c can result in protecting a large number of species (high $\overline{s}$), because the denominator is small. When c is large, additional changes to c will have less of an effect because the denominator of (44) is already large. To some extent, the magnitude of v and k can offset the effects of increasing c.

Forth, the discount factor positively and non-linearly affect the optimal protection level.

Note that discount factors closer to 0 represent a stronger preference for the present than the future (where a δ= 0 means no consideration for the future). A discount factor of 1 implies that the future and present are weighted equally. As the discount factor increase towards 1, the future is weighted more heavily and protecting more species rapidly becomes optimal (at $\delta = 1$, $\overline{s} = +\infty$). Changes in the discount factor, δ, result in the following changes to the optimal protection level:

$$\frac{\partial \overline{s}}{\partial \delta} = -\frac{k(1-\delta) - (k\frac{v}{c} - k\delta)(-1)}{(1-\delta)^2} = \frac{k\frac{v}{c} - 1}{(1-\delta)^2} \tag{45}$$

Next, we examine how our economic criteria – β^* from (28) or the value-to-cost ratio needed for protecting all species to be optimal – varies with the number of critical species (k), the initial number of species present (s_0), and the discount factor (δ).

The number of k critical species can dramatically (non-linearly) reduce β^* (as in Fig. 4 in the main text).

$$\frac{\partial \beta^*}{\partial k} = -\frac{(1-\delta)s_0}{k^2} \tag{46}$$

When k is large, full protection is warranted even if the service value barely exceeds the protection costs. However, when k is small, the difference between the service value and protection costs must be very large to justify protecting everything.

Increases in the initial level of diversity (the size of the species pool s_0) increase β^* linearly:

$$\frac{\partial \beta^*}{\partial s_0} = 1 - \delta \tag{47}$$

This linear relationship between s_0 and β^* implies higher values relative to costs are needed for protecting all species to be economically optimal for larger species pools. When the future is weighted equally with the present ($\delta = 1$), increasing s_0 has no effect on β^*.

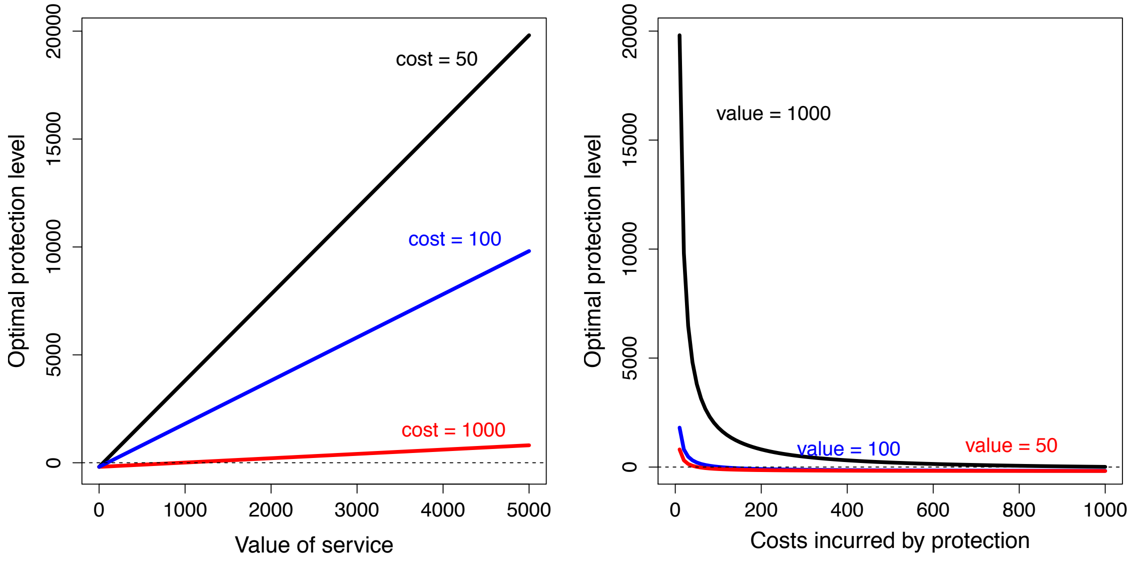

Figure S3: Management and opportunity costs dramatically (non-linearly) influence the optimal level of protection whereas increasing the per-period value of the service only increases the optimal protection level linearly. These graphs compare how the optimal protection level $\overline{s}$ varies as a function of a) the per-period value from the service and b) the costs incurred by protection (direct and indirect) where $k = 10$ and $\delta = 0.95$. The current literature emphasizes valuation of ecosystem services with less of a focus on estimating opportunity and management costs. This analysis suggests that such costs may merit more research, as they may more dramatically influence the level of species protection that is optimal from the standpoint of services than simply increasing the value. When costs are relatively low, the exact level of costs can have a dramatic effect on the optimal level of protection.

Finally, increasing the discount factor linearly decreases the β^* needed for protecting everything to be optimal. The slope of this relationship depends on the fraction of species providing the service (Fig **??**). When all species are critical to the service, meaning $\frac{k}{s_0} = 1$, changing the discount does not affect β^*, and $\beta^* = 1$.

$$\frac{\partial \beta^*}{\partial \delta} = 1 - \frac{s_0}{k} \tag{48}$$

3 Numerical analyses of different relationships between service level and number of species

The literature examining how ecosystem functioning depends on species richness suggests that the level of an ecosystem function is a smooth, non-decreasing function of the number of species [2, 3, 4, 5, 6, 7, 8]. The shape of this relationship is a focus of empirical work (e.g., reviewed in Cardinale et al. [7]) given the implications for how changes in the number of critical species will affect the levels of ecosystem functions and services.

Discussion continues over the exact form of this relationship across systems and scales. Some data syntheses, based on short-term studies, have suggested that the relationship between biodiversity and certain ecosystem functions should be concave and asymptotic (e.g. for biomass production and nutrient cycling; see [4, 7, 9]). This form implies that the loss of species at higher levels of diversity has a smaller impact on the level of a function than the impact at lower levels of diversity [10, 4]. Other studies based on longer-term experiments [3, 5] or synthesizing marine biodiversity-productivity experiments [11] suggest the relationship is closer to linear. In contrast, marine studies in natural (non-experimental) systems, such as in coral reefs and the deep-sea nematode communities, suggest the relationship between functioning and species richness is convex [6]. If these relationships extend to services at management-relevant scales, the current period payoff from a single service in each time period could be represented as some linear, convex, or concave function of the number of remaining species that provide that service.

We can explore the consequences of these different empirical observed relationships for the optimal level of biodiversity protection. To do so, we approximate solutions (optimal policies) for several non-decreasing relationships between the level of a service and the number of critical species providing it that persist in the species pool. We introduce a new state variable, r, to denote the number of critical service providers remaining at some functional level after species are lost. Now, the amount of current period payoff from a service, $f(r)$, depends on the number of critical species providing it r, and is represented by the function υ_r. The state variables that a manager observes are now both s (the total number of species in the species pool) and r (the number of critical species in the species pool). We find the optimal level of species protection for the following model setup.

3.1 Mathematical formulation

Let the current period payoff be denoted by $\{\upsilon_r\}_{r\in\mathbb{N}}$ and in a family such that[5]

$$r \in \mathbb{N} \mapsto \upsilon_r \text{ is non-decreasing,} \tag{49a}$$

$$r \in \mathbb{N}^* \mapsto \upsilon_r - \upsilon_{r-1} \text{ is non-increasing,} \tag{49b}$$

$$\upsilon_r > c > 0 \ , \ \forall r \in \mathbb{N} \ . \tag{49c}$$

In §1.4, we had $\upsilon_r = 0$, for all $r < k$, and $\upsilon_r = \upsilon$, for all $r \geq k$.

Let $\{p_r(s)\}_{0\leq r\leq s}$ be a family in $[0,1]$ such that

$$s \in \{r, r+1, \ldots\} \mapsto p_r(s) \in [0,1] \text{ is non-decreasing,} \tag{50a}$$

$$r \in \{0, \ldots, s\} \mapsto p_r(s) \in [0,1] \text{ is non-increasing,} \tag{50b}$$

$$p_r(r) = 0 \ . \tag{50c}$$

The quantity $p_r(s)$ represents the probability of losing one of the $s - r$ non-critical species in a pool of s species: $p_r(s) = (s-r)/s$. The probability $p_r(r) = 0$ means that if you have exactly r species in the pool, then the probability of losing a species that does not provide the service is 0. Some reduction in value will result – but not a complete loss of the service.

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[5] Notice that (49b) means that $r \in \mathbb{N} \mapsto \upsilon_r$ is concave.

At each time $t = 0, 1, \ldots$, running from 0 to $+\infty$, the manager must choose between two options ($d \in \{NP, P\}$) to manage a pool of s species with r critical species ($r \leq s$):

- either she protects the pool ($d = P$), at cost c, and obtains the ecosystem service of value with certainty $\upsilon_r > c$ during the period $[t, t+1[$;
- or she does not ($d = NP$), and she will either
  - functionally lose one of the $s - r$ non-critical species, with probability $p_r(s)$, and obtain the ecosystem service of value υ_r during the period $[t, t+1[$,
  - or functionally lose one of the r critical species, with probability $1 - p_r(s) = \frac{r}{s}$ and obtain υ_{r-1}.

Therefore, the *expected current period payoff* is

$$U_r(d, s) = \begin{cases} \upsilon_r - c & \text{if } d = P \ , \\ p_r(s)\upsilon_r + (1 - p_r(s))\upsilon_{r-1} & \text{if } d = NP \ . \end{cases} \tag{51}$$

We introduce the *Bellman function* for this problem setup. By definition, $J_r(s)$ is the largest intertemporal payoff

$$J_r(s) = \max_{(d_t)_{t=0,\ldots,+\infty}} \sum_{t=0}^{+\infty} \delta^t U_{r_t}(d_t, s_t) \ , \tag{52a}$$

achieved over all possible sequences $(d_t)_{t=0,\ldots,+\infty}$ of decisions $d_t \in \{NP, P\}$, where the number s_t of species in the pool at time t follows the dynamics

$$s_0 = s \text{ and } s_{t+1} = \begin{cases} s_t & \text{if } d_t = P \ , \\ s_t - 1 & \text{if } d_t = NP \ . \end{cases} \tag{52b}$$

and the number r_t of critical species in the pool at time t follows the dynamics

$$r_0 = r \text{ and } r_{t+1} = \begin{cases} r_t & \text{with probability } p_{r_t}(s_t), \\ r_t - 1 & \text{with probability } 1 - p_{r_t}(s_t). \end{cases} \tag{52c}$$

The Bellman function is solution of this Bellman equation:

$$\begin{aligned} J_r(s) =& \max\{\upsilon_r - c + \delta J_r(s); \\ & p_r(s)[\upsilon_r + \delta J_r(s-1)] + (1 - p_r(s))[\upsilon_{r-1} + \delta J_{r-1}(s-1)]\} \ , \\ & \forall s = 1, \dots, s_0 \ , \end{aligned} \tag{53a}$$

$$J_r(0) = 0 \ . \tag{53b}$$

3.2 Functional relationships between species and the service value

We model several forms for how the current period payoff can depend on the number of critical species (51) based on empirical studies. We use a power function to represent the current period payoff given its flexibility to capture linear, convex, and concave relationships and its mathematical properties (following Reich et al. [5], Mora, Danovaro & Loreau [6]). The function here is $\upsilon_r = ar^b$ for the current value from a service υ_r arising from r service-providing species. For a linear relationship, $b = 1$. For concave relationships, $b < 1$. For convex relationships, $b > 1$. With a $b > 1$, even small changes in the number of critical species can dramatically alter ecosystem service levels. In contrast, when the relationship is concave, the level of a service will only change dramatically when few species remain.

Parameters for the relationship between diversity and the levels of services *per se* are currently unknown. While previous studies primarily measure ecosystem function as the response variable rather than services $perse$, their parameter estimates provide a useful starting point for this model framework. Therefore, we use parameter estimates of b (from Reich et al. [5], Mora, Danovaro & Loreau [6], Cardinale et al. [7]). Because these parameters may be higher or lower for *services*, we explore a range of parameter values for b in (55) and therefore a range of functional relationships. When estimates of parameters defining this relationship for services improve, they can be used in a straightforward manner with our approach.

3.2.1 Linear relationship between species and the service value

If the level of service depends linearly on the number of r species in the pool that can provide the service, the *expected current period payoff* is

$$U_r(d,s) = \begin{cases} ar - c & \text{if } d = P \ , \\ p_r(s)ar + (1 - p_r(s))a(r-1) & \text{if } d = NP \ . \end{cases} \tag{54}$$

3.2.2 Concave and convex relationships between species and the service value

Convex versus concave relationships between diversity and ecosystem functioning have very different ecological implications of biodiversity change. But *do these differences dramatically alter the optimal policy of biodiversity protection for ecosystem services?*

If the level of service depends smoothly on the number of r_t critical species that can provide the service, we use a power function to represent *expected current period payoff*:

$$U_r(d, s) = \begin{cases} ar^b - c & \text{if } d = P \ , \\ \\ p_r(s)ar^b + (1 - p_r(s))a(r-1)^b & \text{if } d = NP \ . \end{cases} \tag{55}$$

We explore a range of parameter for b in (55), including estimates from previous studies on ecosystem functioning [5, 6, 7].

3.3 Numerical results

We solve the Bellman function (53) to approximate the optimal policy using a standard *value iteration* algorithm and R software. We adopt the convergence criteria from Boutilier, Dearden & Goldszmidt [12] as recommended by Marescot et al. [1]: we stop the algorithm when the difference between two value function approximations is less than $\frac{\epsilon(1-\delta)}{2\delta}$, with $\epsilon = 0.0001$.

Results are consistent for different smooth relationships between service level and number of species v_r. Again, it is never optimal to protect species when costs outweigh the maximum value from a service. When the value exceeds the costs, the optimal policy is not to protect the species pool until the number of species (s_t) declines to a critical threshold. Each level of r_t critical species providing the service has a corresponding threshold of s_t at which protecting is optimal for a range of reasonable conditions.

The exact number of s_t species it is optimal to protect will also depend on the parameters of the power function, the discount factor, and the costs incurred by management. Holding other variables constant, lower discount factors (i.e., increasing how much society values the present versus the future) and higher costs of protection both reduce protection levels. For a given r_t, increasing the α parameter of the power function increases optimal protection levels, holding other variables constant (Fig S4).

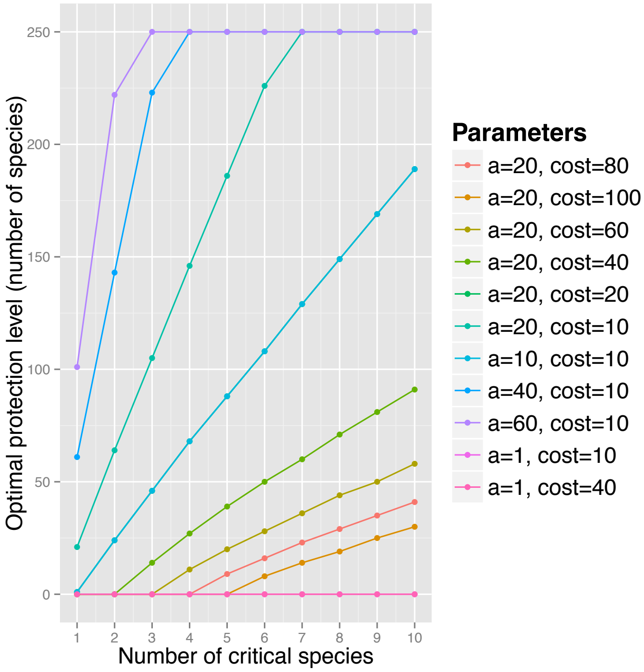

Figure S4: Numerical results for linear relationship ($b = 1$) varying the costs and the a parameter of the power function. The total number of species is 250 and the total number of critical species is 10.

We compared optimal level of species protection for concave, convex, and linear relationships between the number of critical species and the level of the service. We find the optimal policy for various values of the b parameter of the power function. This comparison provides insight into how the optimal level of protection depends on the shape of the relationship – how changes in the number of critical species will alter the level of an ecosystem service (Fig S5). Higher values of b typically result in higher levels of protection except when the relationship between service value and critical species is extremely concave (e.g., approximately $b < 0.25$) and only one critical species remains in the species pool. At that point, since the loss of service value will be the greatest when the number of critical species declines from $r_t = 1$ to $r_t = 0$, protection levels are higher for b < 0.25 when $r_t = 1$. Therefore the optimal policy is not strictly monotonic and increasing with the number of critical species, r_t.

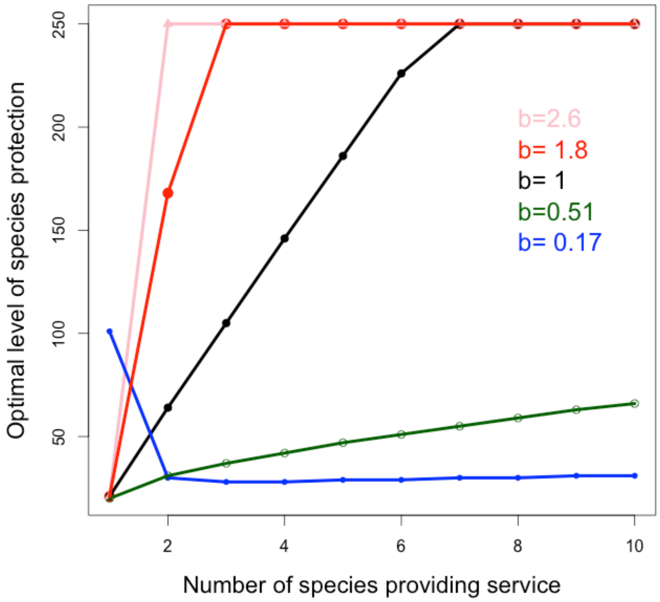

Figure S5: Optimal protection levels for different shapes of the relationship between the level of an ecosystem service and the number of critical species providing it (r_t). We approximate the optimal policy (in number of species) when such current period ecosystem service payoffs follow a power function with different b parameters dictating its shape. [5] estimate b can range between $b = 0.17$ and $b = 0.51$ depending on the number of years considered. For standing stock of biomass (g/$50m^2$), [6, 13] estimated $b = 1.8$ for the Caribbean and $b = 2.8$ for the Eastern Pacific. We show results holding other parameters constant (i.e., for a cost of 10, an initial species pool size of 250 species, a maximum of 10 critical species present in the pool, and a parameter from the power function $a = 20$).

4 SI for case study examples in Fig. 4 and Table S1

Fig. 4 (main text) illustrates variation in the economic criteria required for protecting all species to be optimal (i.e., $\frac{v}{c} \geq \beta^*$) that arise from empirical estimates of the fraction of critical species for those services and locations. We review the information presented in Fig. 4 below and in Table S1. Figure 4 presents averages for estimates of total species (s_0) and number of critical species (k), yielding an average for β^*, but Table S1 shows the range of values resulting from different estimates. The fraction of species directly involved in service provisioning can vary dramatically across services and locations, with important consequences for the economic criteria determining when full biodiversity protection is optimal. This criterion, β^*, also depends on the discount factor (preference for the present versus future). Table S1 shows that lower discount factors (i.e., greater preference for the present versus the future) will require larger ratios of value-to- costs to motivate comparable levels of biodiversity protection.

Wave attenuation in coastal estuaries

Carpentaria Salt Marsh, California, U.S.A.

Estimates of the total number of species (s_0) were obtained from a highly resolved food web ([14]). Hechinger et al. (2011) note that these estimates for total number of species may be low because several nodes may be missing, under-represented or severely aggregated (specifically plant ecto- and endo-parasites, bird ectoparasites, free-living protists, meiofauna, fungi, bacteria, etc.; see [14] for details). Since increasing s_0 leads to a consequent increase in β^*, this β^* may therefore represent a low estimate.

The number of critical species directly critical to the provision of coastal protection services in this salt marsh range from $k = 1$ to 5 (5 is the total number of marsh halophytes occurring in this location according to Zedler, Callaway & Sullivan [15]). Table S1 presents this range for k. At any given point in time, such as when facing future global change, there is uncertainty over which species will dominate and produce the bulk of the service. There is further uncertainty over how the presence and number of these critical species maps to value produced by services in this ecosystem. Given that the different species can provide wave attenuation, this service may be better represented by a smooth payoff function.

Carbon storage in forests

Tropical Dry Forest of the Montes Azules Biosphere Reserve, Mexico

Balvanera et al. (2005) estimated that only 13% of the total tree species present provided 90% of carbon storage in the study year at the Montes Azules Biosphere Reserve in Southeast Mexico ([16] Balvanera, Kremen, and Martinez-Ramos 2005). This study reported a total of 169 trees in the Reserve, therefore 13% is about $k = 22$ species. To maintain <90% of carbon storage, k will be lower. To maintain high fractions of total aggregate of carbon storage over a longer time horizon, a larger proportion of tree species may be required as rank abundances of species change.

We estimate β^* for a range of total number of species present (s_0). Parkswatch [17] estimates 1779 animals (114 mammals, 77 snakes and amphibians, 112 fishes, 341 birds, 1,135 invertebrates) in Montes Azules. For plants, estimates range from 392 woody species documented at the Chajul Field Station (within the Montes Azules Biosphere Reserve in Lacanda), and 3,400 vascular plant species identified in the Selva Lacandona region [18]. This provides a range of s_0 : 2171-5179 species. As many species may not be identified, these numbers likely represent low estimates for the total number of species present [17]. Low estimates for the total number of species translate to low estimates for how many times greater the service value needs to be relative to the costs in order for full protection to be optimal.

Pollination services for watermelon crops, multiple locations, U.S.A.

Yolo County, California

Out of a possible set of 192 native bee species, 30 can contribute to watermelon pollination [19], with as few as 2 bee species providing ample pollination in 2001 [20]. The composition and rank order of species providing the bulk of the pollination service changes from year-to-year, creating uncertainty over which species are critical at any given point in time in the future. Given the importance of native vegetation as habitat for pollinators, the species indirectly critical to support this service are likely greater [21]. Estimates of the total California Upland species pool range (s_0) from 1075 to 2040 [22, 23, 24]. [6]

New Jersey and Eastern Pennsylvania, U.S.A.

Central New Jersey and Eastern Pennsylvania farms are located within temperate, mixed oak forests. Between 6-46 species of pollinators sufficiently pollinate watermelon crops at the farms surveyed by Winfree et al. [25]. Some farms could be sufficiently pollinated by only one bee group: bumblebees ($k = 6$ species) or small bees ($k = 27$ species). Winfree et al. (2007) also estimate that 46 native bee species could sufficient pollinate watermelon crops at 91% of the farms surveyed (such as when compensating for domesticated pollinator losses). Abundance of different species will clearly influence the size of the critical subset required to fully pollinate watermelon crops. Thus, we consider we consider the size of the subset of critical species to range from the minimum number of species record to fully pollinate watermelon ($k = 6$) to all 46 that can pollinate watermelon crops.

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[6] These estimates have been compiled from multiple sources and are likely low, given the number of species groups unaccounted for in these habitats (e.g., amphibians, invertebrates, some parasite groups, etc.).

Within these mixed oak forest ecosystems, the species pool is estimated to be more than 1338 plants and animals [25, 26, 27].This estimate may be low (e.g., under representing parasites or other invertebrates); therefore, we likely present a low estimate of β^* meaning the value would have to be even greater than the costs of management to justify protection of all species.

Carbon storage in mangroves, multiple locations

Sundarban, India

Gopal and Chauhan (2006) summarize the total biodiversity recorded for the Sundarban region ($s_0 = 1722$) [28]. The number of mangrove organisms directly contributing to carbon storage is estimated to be $k = 30$ to 36 [28, 29]. This estimate of the number of directly critical species includes mangrove species but could also encompass associated organisms on which productive mangroves and their ability to store carbon depend. For instance, crabs or soil biota can facilitate carbon storage but the identity of all of these critical species may be uncertain [30, 31, 32]. Thus this k may represent a lower bound and β^* may be lower.

Deluge Inlet, Hinchinbrook channel, Queensland, Australia

In Deluge inlet, a food web study recorded a minimum of 71 species [33]. Clough (1998) recorded 4 species of mangroves storing carbon in this location [34].

Grasslands: various ecosystem functions underpinning services

Multiple locations (Minnesota, U.S.A. and Europe from Isbell et al. [35])

Isbell et al. [35] analyzed data from 17 grassland experiments that measured different ecosystem functions underpinning grassland services from multiple locations, years, and under different environmental conditions. These functions included net nitrogen mineralization, root biomass and nitrogen, soil nitrogen content, nitrogen uptake, and others (see Isbell et al. [35] Supplemental Data for details). They found that 27% of plant species within a given context (location, year, and for a particular function) were required to promote ecosystem (regardless of species pool size) [35]. Thus, we use a fraction of critical species of 27% to determine β^* for the grasslands in Isbell et al. [35].

A Technical lemmas

We say that a function g is decreasing if $x > y \Rightarrow g(x) > g(y)$.

Lemma 1. *Let* $\mathbb{X} \subset \mathbb{R}$, f *be a function* $f : \mathbb{X} \mapsto \mathbb{R}$ *and assume that*

1. f *admits a fixed point* $\overline{a} \in \mathbb{X}$*, that is,* $\overline{a} = f(\overline{a})$*,*
2. $x \in \mathbb{X} \mapsto f(x) - x$ *is decreasing.*

Then, $\overline{a}$ *is the unique fixed point of* f*, and we have the equivalence*

$$a = \max\{f(a), b\} \iff a = \max\{\overline{a}, b\} \ . \tag{56}$$

Proof. By assumption 2, if f has a fixed point, it is unique.

Before proving the equivalence (56), we show the following property:

$$\overline{a} \geq b \iff b \leq f(b) \text{ and } \overline{a} \leq b \iff b \geq f(b) \ . \tag{57}$$

Indeed, we have that

$$\begin{aligned} \overline{a} > b \Rightarrow \quad & f(\overline{a}) - \overline{a} < f(b) - b && \text{since } x \mapsto f(x) - x \text{ is decreasing} \\ \Rightarrow \quad & b < f(b) && \text{since } f(\overline{a}) - \overline{a} = 0. \end{aligned}$$

In the same way, we prove that $\overline{a} < b \Rightarrow b > f(b)$.

Now, we turn to proving the equivalence (56). First, we prove that $a = \max\{\overline{a}, b\} \Rightarrow a = \max\{f(a), b\}$ by considering two cases.

- Suppose $\overline{a} \geq b$ and $a = \max\{\overline{a}, b\}$.

  In that case, we have $a = \max\{\overline{a}, b\} = \overline{a}$ and therefore

  $$\begin{aligned} \max\{f(a), b\} = \quad & \max\{f(\overline{a}), b\} && \text{since } a = \overline{a} \\ = \quad & \max\{\overline{a}, b\} && \text{since } f(\overline{a}) = \overline{a} \text{ by assumption 1} \\ = \quad & a && \text{since } a = \max\{\overline{a}, b\} = \overline{a}\ . \end{aligned}$$

  Hence, we have proved that $(a = \max\{\overline{a}, b\}$ and $\overline{a} \geq b) \Rightarrow a = \max\{f(a), b\}$.

- Suppose $\overline{a} \leq b$ and $a = \max\{\overline{a}, b\}$.

  In that case, we have $a = \max\{\overline{a}, b\} = b$ and therefore

  $$\begin{aligned} \max\{f(a), b\} = \quad & \max\{f(a), a\} && \text{since } a = b \\ = \quad & a && \text{from (57) since } \overline{a} \leq a = b\ . \end{aligned}$$

  Hence, we have proved that $(a = \max\{\overline{a}, b\}$ and $\overline{a} \leq b) \Rightarrow a = \max\{f(a), b\}$.

Second, we prove that $a = \max\{f(a), b\} \Rightarrow a = \max\{\overline{a}, b\}$.

- Suppose $f(a) \geq b$ and $a = \max\{f(a), b\}$.

  In that case, we have $a = \max\{f(a), b\} = f(a)$ and therefore $a = \overline{a}$ since $\overline{a}$ is the unique fixed point of f. We conclude that

  $$a = \overline{a} = \quad \max\{\overline{a}, b\} \quad \text{since } \overline{a} = a = \max\{f(a), b\} \geq b \ .$$

  Hence, we have proved that $(a = \max\{f(a), b\}$ and $f(a) \geq b) \Rightarrow a = \max\{\overline{a}, b\}$.

- Suppose $f(a) \leq b$ and $a = \max\{f(a), b\}$.

  In that case, we have $a = \max\{f(a), b\} = b$ and therefore $a = b = \max\{f(a), b\} \geq f(a)$ implies, by (57), that $a = b \geq \overline{a}$. We conclude that $a = b = \max\{\overline{a}, b\}$.

  Hence, we have proved that $(a = \max\{f(a), b\}$ and $f(a) \leq b) \Rightarrow a = \max\{\overline{a}, b\}$.

This ends the proof. □

Lemma 2. *Let* $\mathbb{S} \subset \mathbb{N}$ *and let* A*,* B*, and* C *be three functions* $\mathbb{S} \to \mathbb{R}$*. We define*

$$\overline{s} = \min\{s \in \mathbb{S} \mid B(s) \geq C(s)\} \ , \tag{58}$$

with the convention that $\min \emptyset = +\infty$*.*

Suppose that $s \in \mathbb{S} \mapsto B(s) - C(s)$ *is non-decreasing. Then,*

$$A(s) = \max\{B(s), C(s)\} \iff \begin{cases} A(s) = B(s) \ , & \text{if } s \geq \overline{s} \ , \\ A(s) = C(s) \ , & \text{if } s < \overline{s} \ . \end{cases} \tag{59}$$

Proof. We consider two cases: $\overline{s} = +\infty$ and $\overline{s} < +\infty$.

When $\overline{s} = +\infty$, we deduce from (58) that $B(s) < C(s)$, $\forall s \in \mathbb{S}$. Hence

$$\max\{B(s), C(s)\} = C(s) \ , \ \forall s < \overline{s} = +\infty \ .$$

When $\overline{s} < +\infty$, we deduce from (58) that $B(s) < C(s)$, $\forall s < \overline{s}$, and that $B(\overline{s}) \geq C(\overline{s})$. Since $s \in \mathbb{S} \mapsto B(s) - C(s)$ is non-decreasing, we have that $B(s) \geq C(s)$, $\forall s \geq \overline{s}$. Therefore,

$$\max\{B(s), C(s)\} = \begin{cases} B(s) \ , & \text{if } s \geq \overline{s} \ , \\ C(s) \ , & \text{if } s < \overline{s} \ . \end{cases}$$

This ends the proof. □

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II. Factors aligning ecosystem service and conservation goals

Introduction

A major global challenge is halting the decline of both biodiversity and the benefits it provides to humans (i.e., ecosystem services). These dual objectives (preserve biodiversity and maximize the value of services ecosystems provide) raise the question whether management strategies targeting ecosystem services versus management strategies targeting biodiversity conservation align (Millennium Ecosystem Assessment 2005; Anderson *et al.* 2009; Polasky *et al.* 2012a). If strategies typically align, focusing on one objective will benefit the other. If there are situations where they do not align, however, then people or institutions who focus solely on one objective may drive outcomes that are unacceptable to those seeking the other objective. Individual case studies suggest that each alternative is plausible (Adams 2014). In some settings, managing for ecosystem services also creates broad conservation benefits – a win-win outcome -- such as in Oregon, U.S.A. (Nelson *et al.* 2009). However, other studies find that optimizing ecosystem services does not necessarily meet conventional conservation objectives (e.g., protecting threatened species or biodiverse locations) nearly as well as managing specifically for conservation (Chan *et al.* 2006; Naidoo *et al.* 2008; Polasky *et al.* 2012a). Such uncertainty about conservation outcomes has prompted fears by some conservation biologists that shifts towards ecosystem services as the primary objective may provide few benefits to biodiversity conservation (e.g., McCauley 2006). Rather than viewing this issue as a polarized choice between two options, however, we could achieve better outcomes through a more nuanced solution. If ecosystem service objectives and biodiversity objectives do align in some cases and not in others, a more impactful conclusion would be that we can achieve better outcomes from anticipating the settings where these two objectives align and where they do not. With such knowledge, we can identify when a sole focus on the economic benefits of ecosystem services is sufficient to also conserve biodiversity and when economic objectives alone would put biodiversity at risk. Distinguishing among these two outcomes is critical to guide policy initiatives like the intergovernmental platform on biodiversity and ecosystem services (IPBES).

To this end, Dee et al. (*2015*) developed a theoretical framework for forecasting the optimal level of biodiversity protection that arises solely from the economic incentives of ecosystem services. The goal of this analysis was not to argue that economic decisions alone should guide decisions, but rather to identify those situations where people or institutions who place intrinsic value on biodiversity need to take action versus where their interests will be adequately addressed by a focus on the economic benefits of ecosystems to people. They identify several factors that strengthen alignment between service and conservation objectives and several others that do not.

Costs incurred by biodiversity protection are a fundamental constraint on when the two objectives will align. The costs include both the direct costs of species protection and the opportunity costs of preventing other uses or activities. At one extreme, a focus on ecosystem services alone will provide no incentive for species protection if the cumulative value of all services does not exceed these costs. More often, however, the optimal economic strategy is to wait to invest in biodiversity protection. Waiting avoids significant protection costs, but it risks losing service value. As biodiversity declines, the risk of service losses increase and can eventually outweigh the more certain costs of ongoing protection.

The resulting level of biodiversity protection that is economically optimal depends on two key features of an ecosystem's ecology. First, the smaller the fraction of species that play critical direct or indirect roles in providing service values, the more service values must exceed protection and opportunity costs to economically justify protecting all species. Second, if the economic value of the services produced saturates quickly with the number of species providing the service, the alignment between service values and conservation is also weakened. The theory underlying this second point supports the intuition of several previous authors about the consequences of value gains that diminish as biodiversity increases (Ehrlich & Ehrlich 1981; Schwartz *et al.* 2000; Srivastava & Vellend 2005; Cardinale *et al.* 2011).

On the positive side, several factors can increase the economic incentives for biodiversity protection provided by ecosystem services. Intriguingly, a factor strengthening the alignment between conserving biodiversity and obtaining ecosystem services is uncertainty over which species provide the services. Despite the potentially large costs incurred by protection and the significant financial opportunities that might be lost, Dee *et al.* (2015) showed that full biodiversity protection can be economically optimal even if only a small fraction of species are critical *if* there is large uncertainty in the identity of these key service providers. With great uncertainty, full protection becomes economically optimal even when most species play no service roles at all, because the risk of losing services cannot be reduced by focusing management actions solely on known service providers. A second factor that enhances alignment is multiple services. Ecosystems provide diverse services, and optimizing for multiple services from an ecosystem can also greatly increase the economically optimal level of protection (Dee *et al.* 2015), especially if different services depend critically on different species.

In this review, we ask if there are other key factors that may enhance the alignment between conserving biodiversity and obtaining ecosystem services than might be expected by skeptical conservation biologists (e.g., McCauley 2006; Adams 2014). We examine four potentially important issues. First, is the number of species that are important contributors to services much larger than many current estimates (e.g., Kleijn *et al.* 2015; Fauset *et al.* 2015). For the vast majority of ecosystem services in natural ecosystems, estimates of critical species come solely from observational studies. We explore insights from those systems with more definitive experimental studies to ask if observational estimates are consistently too low (e.g., Tilman *et al.* 2001; Cardinale *et al.* 2011, 2012; Isbell *et al.* 2011a; Reich *et al.* 2012; Gamfeldt *et al.* 2013). Second, management actions to enhance ecosystem services can take many forms. Some are relatively generic actions, such as protecting a location or restoring a habitat type, that may enhance services while also providing other incidental conservation benefits at no additional cost (Anderson *et al.* 2009). Third, if the species most at risk of local extirpation also contribute significantly to one or more services, managing for services should provide broader benefits to biodiversity by disproportionately protecting at-risk species. This issue could also work in the opposite direction, however, if rare or threatened species play little role in most services (Srivastava & Vellend 2005; Adams 2014; Kleijn *et al.* 2015). Fourth, managing for even a single, relatively low value ecosystem service can have broader indirect benefits to biodiversity if the species that are significant to service provision have functional ecosystem roles that promote broader biodiversity benefits (e.g., if they are habitat forming species or keystone predators; Power *et al.* 1996; Hacker *et al.* 1997).

1. What fraction of species play key roles in producing ecosystem services?

The proportion of species in an ecosystem that are critical to providing services plays a foundational role in how well service and biodiversity objectives align. If all species were important to service provision, these objectives would be the same. Yet, if most species play no functional role in the provision of any service, biodiversity protection would rarely make sense for a manager tasked solely with maximizing the service benefits of ecosystems to people. Where most ecosystems lie with respect to the fraction of species that play important service roles is the key question. For nearly all ecosystem services in most natural ecosystems, our understanding of the functional service roles of different species comes entirely from conjecture based upon observational studies. Although purely observational studies typically provide very limited insight on species roles, they commonly conclude that many services are provided by a very small fraction of the species in that system (e.g., Kleijn *et al.* 2015; Ngo *et al.* 2013; Fauset *et al.* 2015). For instance, Balvanera *et al.* (2005) estimated that only 13% (around 22 species) of all tree species provided 90% of above-ground carbon storage in the Montes Azules Biosphere Reserve, Mexico. Similarly, around 1% of the estimated 16,000 tree species in Amazonian forests provide around 50% of total tree carbon storage (ter Steege *et al.* 2013; Fauset *et al.* 2015). A recent synthesis of crop pollination by native species shared a similar conclusion: 2% of roughly 6,000 native pollinators provide 80% of the value of pollination services for 20 crops across continents (Kleijn *et al.* 2015). On the one hand, these small fractions may be overestimating the fractions of critical species in the ecosystem, because they only consider a subset of taxa (e.g., just the trees, or just the pollinators) rather than the total ecosystem diversity. On the other hand, the limitations of estimates purely from observations may be missing large numbers of species that play unacknowledged roles.

One inherent limitation of observation studies is that they commonly associate the level of contributions to a service by a species as a function of its abundance (e.g., the abundance of native pollinators – Winfree *et al.* 2015; or the biomass of vegetation for coastal protection from salt marshes – Shepard *et al.* 2011; Table 2). Since abundance is heavily skewed in most systems, a few species are presumed to account for most service contributions (Walker *et al.* 1999; Smith & Knapp 2003; Lyons *et al.* 2005, Winfree *et al.* 2015). These conclusions may be compromised by several factors. First, the abundance of a species is not static. It is determined by numerous interactions and feedbacks in multi-species ecosystems, and dominance can change as environmental conditions shift. Such dynamics are difficult to capture in any single snapshot observation of a system; for instance, feedbacks might occur over longer time horizons. Second, observational studies cannot assess whether the dominance of an abundant species depends upon other rarer species in the ecosystem. However, long-term experiments in grasslands show that more diverse plots can support a greater overall biomass even though much of the diversity is relatively rare (Tilman *et al.* 2001).

For a few ecosystem services in a few systems, these limits of observational studies have been overcome by experiments that manipulate the number and composition of species and measure the consequences for ecosystem functioning (BEF experiments). These BEF experiments typically suggest that estimates from observation studies of the fraction of critical species are too low, and potentially far too low. This discrepancy can be attributed to several factors. First, experiments detect the consequences of removing particular species, which enable more rigorous identification of their functional contributions to services. Extrapolating from functional relationships estimated from hundreds of BEF experiments, Cardinale *et al.* (2011) predict that for biomass production, decomposition, and nutrient uptake the fraction of species required to obtain ecosystem functions at levels higher than 50% of their maxima are higher than previously suggested by intuition from observations (Schlapfer *et al.* 1999) and higher than the number of species used in most experiments. Second, as the time horizon increases, the number of species contributing also increases significantly (Kremen *et al.* 2002b; Reich *et al.* 2012). Although the amount that an ecosystem function increases with an additional species often saturates in the short-term, saturation occurs at a much higher diversity of species in longer-term experiments (Reich *et al.* 2012). Indeed, the results from Reich *et al.* (2012) revealed a large impact of the loss of a single species even for plots containing the maximum number of species used the experiments. Third, considering the full suite of services provided by any ecosystem will increase the number of critical species relative to any single service (Hector & Bagchi 2007; Zavaleta *et al.* 2010; Isbell *et al.* 2011b; Maestre *et al.* 2012; Gamfeldt *et al.* 2013). The more dissimilar the services are, the greater the number of critical species likely grows.

From experimental evidence, we can conclude that a higher percentage of species contribute to services than observational studies might reveal, but two important uncertainties remain: whether these experimental insights 1) extend to all types of services and 2) scale to the far greater numbers of species that occur in natural ecosystem. Due to logistical constraints (e.g., factorial designs that would require astronomically and impossibly large numbers of treatments to include larger numbers of species), experiments have only manipulated a very small subset of the *total* diversity of any ecosystem (Lyons *et al.* 2005; Srivastava & Vellend 2005). Also, experiments typically include species from only one trophic level (e.g., plants – Duffy 2003) and have not manipulated truly rare and threatened species (Lyons *et al.* 2005).

In sum, experiments clearly show that a broader range of species losses can have an effect on ecosystem services than observational insights might suggest. Nonetheless, there is still considerable uncertainty about how large the fraction of critical species is for any service in any ecosystem considering the large number (hundreds to thousands) of species in natural systems. Yet, we can conclude that this fraction is likely much higher than would be estimated for a single service and over a short time horizon. The likely increases are magnified when considering multiple services. Nonetheless, there is still considerable uncertainty about how high the fraction of species critical to at least one service might extend.

For the remaining sections of this paper we examine whether other issues might further extend the alignment of ecosystem service and biodiversity objectives even in those cases where the fraction of critical species is too small to warrant broad biodiversity protection.

2. When do actions for ecosystem services provide conservation benefits?

Management actions are often coarse (e.g., protecting a location or restoring a habitat type), so managing for services may "incidentally" provide broader conservation benefits than the service objectives that motivated the management action. Therefore, alignment is strengthened if the actions taken to maximize ecosystem services also protect biodiversity significantly at no added cost. This issue is best examined in the context of spatial land management. Several studies address whether spatial priorities for conservation and ecosystem service objectives co-occur at regional and global scales. They find mixed results (e.g., Chan *et al.* 2006; Naidoo *et al.* 2008; Anderson *et al.* 2009; Nelson *et al.* 2009; Polasky *et al.* 2012a). In some cases, the management option to maximize the service is to protect places (e.g., in parks) that also create large conservation benefits to all species in that location at no added costs (Nelson *et al.* 2009; Strassburg *et al.* 2012). Therefore, win-win scenarios are possible (e.g., Nelson *et al.* 2009).

Such co-benefits, however, are not the rule. Differences in locations or habitats of management priorities for ecosystem services versus conservation are common (e.g., Chan *et al.* 2006; Naidoo *et al.* 2008; Anderson *et al.* 2009). At a global scale, the places with the highest service values for water provisioning, carbon storage, carbon sequestration, and grassland production of livestock, are often not the places that conservation planning schemes would prioritize for protection (Naidoo *et al.* 2008). In Minnesota, U.S.A., there are also some differences in priorities for land acquisition to optimize biodiversity conservation versus priorities to optimize carbon sequestration and water quality (Polasky *et al.* 2012b). In this case, a focus on managing for these ecosystem services rather than the explicit goal of biodiversity protection would achieve only half of the conservation benefits of a focus on biodiversity protection (Polasky *et al.* 2012b). Similarly, in central California, U.S.A., targeting locations for recreation, carbon storage, pollination, water storage, forage production, and flood control achieves a lower level of biodiversity protection than land planning explicitly designed for conservation benefits (approximately 44% less -- Chan *et al.* 2006).

The degree of overlap in land management priorities for biodiversity and services depends on the set of services considered and the scale analyzed. At a regional scale, in central California, U.S.A., locations for biodiversity conservation were very weakly *negatively* correlated with priorities for pollination and forage production but weakly positively correlated with carbon storage and flood control (Chan *et al.* 2006). For other services, there may be fewer trade-offs, such as for recreation and water storage in California (Chan *et al.* 2006). At the national-scale for Britain, Anderson *et al.* (2009) also found positive, negative, and no associations between species of conservation interest and locations providing the highest levels of carbon storage, annual agricultural income, and recreation (Anderson *et al.* 2009). Depending on the scale and resolution of data considered, their results changed dramatically. At times the relationship even flipped, suggesting that this relationship is not only location but also scale specific. Although such quantitative studies do not exist for many locations, a quantitative synthesis of the existing studies is needed to determine whether there are predictable patterns in which services or locations align or trade-off with conservation priorities.

Restoration of degraded habitats represents another management action that is used to achieve ecosystem service goals that may also derive important biodiversity benefits for species with no role in the service. In studies to date, whether restoration actions benefit *both* biodiversity and ecosystem services varies by location and type of service (reviewed in Bullock *et al.* 2011). Both outcomes are documented – again, varying by case and location (Bullock *et al.* 2011). For instance, restoring vegetation can benefit vulnerable and specialized native pollinators in California, U.S.A (Kremen & M'Gonigle 2015), while enhancing pollination of crops and other ecosystem services, including pest control, by supporting populations of predators and storage of C in soil (Wratten *et al.* 2012). In contrast, in Europe Kleijn *et al.* (2015) demonstrate that managing for pollination services does not consistently align conservation and pollination of crops, because rare and threatened pollinators typically do not occur near agricultural areas. Such alignment also depends on the target of restoration – native versus non-native species and habitats (Bullock *et al.* 2011) – when novel and non-native ecosystems can each provide the required services (see Ewel & Putz 2004; Jackson & Hobbs 2009).

A greater focus on when and where actions for both objectives are the same and when they differ can help identify when managers have opportunities for mutual benefit versus face trade-offs. There are scenarios where the locations that produce the largest values of several services are not highly correlated with locations of conservation priority. The same is true for restoration, especially when considering restoration of novel ecosystems with exotics that produce a target service (Jackson & Hobbs 2009; Bullock *et al.* 2011). The frequency and degree of trade-offs will depend on the set of services and settings considered (Chan *et al.* 2006, Anderson *et al.* 2009). Future quantitative syntheses are needed to determine if alignment varies predictably across studies depending on the services and habitat types— or if it is unique to each location, which would reduce the possibility for simple rules of thumb for managers.

3. Do rare species enhance services?

We next explore the potential roles of rare species in the production of ecosystem services. With respect to the alignment of ecosystem services and conservation, the question is how these rare species affect ecosystem services, because most species are relatively rare in all ecosystems (Rabinowitz *et al.* 1986; Lyons *et al.* 2005), and as a result existing observational studies would typically assume their effects on services are small. For alignment, underestimating the roles of rare species on services is problematic, because these rare species will include the species most in need of conservation interventions since they face a greater risk of loss due to ongoing anthropogenic threats or to demographic or environmental stochasticity (Pimm *et al.* 1988; Smith & Knapp 2003; Jain *et al.* 2014).

Despite their rarity, such species could contribute significantly to the value of a service currently, or if they became more abundant (Lyons *et al.* 2005). Thus we need to examine the pools of rare species with respect to how they fit into three categories: rare species that: 1) currently contribute directly or indirectly to services; 2) have contributed to services in the past when they were more abundant (and hence could presumably contribute in the future if they were more abundant); and that 3) do not contribute significantly to any ecosystem services. The distribution of rare species in these three groups has important implications for the alignment between ecosystem service and conservation objectives.

3.1 Rare species that currently contribute

Some rare species currently contribute to ecosystem services, either directly or indirectly. Directly, rare species can provide a service when they have highly specialized or unique functional roles, such as in the case of highly specialized pollination systems. For example, production of figs relies on a highly specialized and obligate mutualistic relationship between fig trees (*Ficus* spp.) and relatively uncommon fig wasps (Chalcidoidea) (Machado *et al.* 2005). Further, around 18 pollinators in Germany, the Netherlands, Sweden, and the United Kingdom are currently rare and threatened and also contribute significantly to pollination services (representing 5% or more of observed flower visits within a study, Kleijn *et al.* 2015).

There is greater alignment between ecosystem service and biodiversity conservation goals when some rare species contribute significantly to the economic value of the service, especially if there is uncertainty over the identity of these important rare species (Dee *et al*. 2015). Despite the above examples, the functional roles of the vast diversity of rare species in most ecosystems is highly uncertain (Lyons *et al.* 2005; Jain *et al.* 2014).

3.1.1 Indirect contributions of rare species

Rare species can also contribute indirectly to a service. First, they can modify the local environmental conditions in ways that benefit service providers (reviewed in Lyons *et al.* 2005). The best example is relatively rare N-fixing species that enhance soil nutrient cycling and availability. The presence of these N-fixing species supports higher overall biomass production through time in grasslands (Reich *et al.* 2012), which is associated with higher yields for biofuels (Tilman *et al.* 2006). Similarly, in an Alaskan shrub wetland**,** relatively rare *Equisetum spp*. (5% of the communities' biomass) acquire and cycle P, K, and Ca more efficiently and enhance nutrient availability for uptake by dominant species (Marsh *et al.* 2000).

Rare species may also be keystone species or predatory species that play a disproportionate role in structuring communities and thereby indirectly contribute to one or more services (Lyons *et al.* 2005; Srivastava & Vellend 2005). For instance, in Aluetian kelp forests, keystone predators (e.g., sea otters *Enhydra lutris*) can indirectly enhance or support carbon storage (Wilmers *et al.* 2012). By limiting the abundance of sea urchins (*Strongylocentrotus* spp.) that can overgraze kelp biomass (Estes & Duggins 1995; Steneck *et al.* 2002), the presence of sea otters indirectly modifies kelp distributions and biomass, which can dramatically increase biomass, productivity, and C storage (Reed & Brzezinski 2009; Wilmers *et al.* 2012). This has implications for the consequences of removing rare predators for services. In New England, U.S.A. salt marshes, removal of relatively uncommon predators can indirectly cause marsh die-off, with potential consequences for ecosystem services (Bertness *et al.* 2014; Brisson *et al.* 2014).

These cases show that rare species can contribute to some ecosystem services indirectly. Just as in the case of rare species with direct benefits, it is an open question how prevalent these cases are? It is difficult to detect the feedback effects of rare species in both observational studies and short-term experimental studies. Further, experiments typically do not include truly rare species to detect their potential effects on services (Schwartz *et al.* 2000; Lyons *et al.* 2005). This would be a fruitful area for further research.

3.2 Rare species that could contribute at higher abundances

Some species that are currently rare may have contributed to services in the past or could contribute in the future if they were more abundant. This category includes rare species that were previously common because of disease, overharvesting, or habitat loss. This category also includes species that could become more abundant in the future as environmental conditions change. Future increases in abundance might result from targeted management actions (e.g., restoration or reintroduction) or from changing environmental conditions that affect species dominance (e.g., see Walker *et al.* 1999). For this class of rare species, managing for the ecosystem service could provide managers with an incentive to increase their abundances, which strongly aligns ecosystem service and conservation goals.

There are many examples of species that were once abundant and contributed to services in ways they no longer do. Species that were once extremely common, like the American chestnut *Castanea dentata*, once provided services like carbon sequestration and affected the hydrology of nearby streams (Ellison *et al.* 2005). Indeed, historical reductions in the abundance of common species have resulted in not only extinction (e.g., the passenger pigeon; Gaston and Fuller 2008) but also large impacts on the functioning and structure of ecosystems and their services (e.g., lost of foundation species in North American forests; Ellison *et al.* 2005; Gaston & Fuller 2008).

This class of currently rare species could contribute substantially to one or more services today if its abundance increased or recovered. For instance, reintroductions, restoration, and species recoveries have the potential to restore functions and the services they support. In Yellowstone National Park, U.S.A., the combined effects of the re-introduction of wolves and recovery of beaver has influenced services provided by riparian habitats (Vermatt *et al.* 2015). Similarly, many of the world's fish populations have been depleted from overfishing, and recovering fisheries species through improved management enhances not only conservation but also food production and employment opportunities (Worm *et al.* 2009; Costello *et al.* 2012).

Alternatively, rare species that contribute little now may play key roles in the future (Walker *et al.* 1999; Chapin *et al.* 2000; Mouillot *et al.* 2013). Walker *et al.* (1999) posited that abundances of species can "switch" under different environmental conditions so that some rare species become dominant and *vice versa*. There may be future scenarios in which currently rare species with unique trait combinations thrive as conditions change. For example, as the climate changes, currently rare tree species may be better suited to the new conditions and emerge as important contributors to above-ground carbon storage (Mouillot *et al.* 2013; Fauset *et al.* 2015). This pattern could also occur when management or human impacts change. For example, in rangelands rare species became more common under heavy grazing and increased in abundance while the abundance of the dominant species declined (Walker *et al.* 1999). Much less is known about which changes in environmental or management conditions will result in which rare species emerging as significantly contributors to ecosystem services directly or indirectly. This uncertainty enhances the value of biodiversity protection as a hedge for promoting future service benefits.

3.3 Rare species that never contribute

Although rarity does not preclude important functional roles, as the many examples above illustrate, there may also be many rare species that have played and always will play limited roles in the production of all ecosystem services. A focus solely on the economic benefits of ecosystem services would be indifferent to their loss from ecosystems. The key question is whether species in this category are the majority or the minority of rare species. Since we lack information on the functional contributions of most rare, potentially at-risk, species (Lyons *et al.* 2005), we have limited insight into the size of this species category. How many rare species play no role today, never played a role in the past, and will never play a significant role in the future? How many species that are rare in one habitat are common, or even dominant, in another? Would many rare species become highly abundant if one or more currently abundant species were to be harmed by an environmental change? The answers to these questions are important to knowing whether a focus solely on managing for ecosystem services will leave a large pool of at-risk species vulnerable to losses.

Answering these questions is challenging, and we suggest routes for future research. Major challenges in detecting the role of rare species are understanding the consequences of their removal and their potential role under different conditions if their abundance increased -- especially given the large number of relatively rare species. One way to detect the potential effects of rare species is to experimentally increase their abundance and measure the consequences for ecosystem services. However, prioritizing which rare species to include in experiments will be necessary and could be done by considering response and effect traits (Lavorel & Garnier 2002; Larsen *et al.* 2005; Díaz *et al.* 2007; Lavorel *et al.* 2013) or by adapting existing frameworks for bioprospecting and optimal search, used in economics and pharmaceutical research for genetic characteristics. Specifically, bioprospecting and optimal search approaches can guide selection of rare species to include in experimental studies when such “sampling” incurs costs, but the degree of benefits to ecosystem services are uncertain (e.g., Polasky *et al.* 1993, 2005; Costello & Ward 2006). Given logistical and combinatorial constraints of experiments with fully factorial designs, research should also take advantage of natural experiments. Natural experiments can identify drivers of fluctuations in species rarity and dominance through time and space, when coupled with rigorous statistical approaches (e.g., causal inference methods from econometrics, see Angrist & Pischke 2009 for general overview). They can also help understand when these potential changes occur, what drives them (e.g., environmental, management, or community structure variables), and their consequences for service provisioning at a larger scale, Further, natural experiments provide valuable data to test predictions from small-scale experiments at more relevant spatial scales.

4. Do Service Providers Also Benefit Biodiversity?

Managing solely to obtain an ecosystem service could provide broader conservation benefits if the key service providers also play key roles in the ecosystem that benefit other species. Conservation outcomes could be achieved even if management is focused myopically on optimizing a single (relatively low value) service in a relatively low diversity ecosystem. For example, if service providers also provide critical habitat or act as keystone species (Power *et al.* 1996; Hacker *et al.* 1997) managing for services will have added biodiversity benefits at no cost. To address this issue, we reviewed many case studies of several regulating ecosystem services – pollination of crops, coastal protection from salt marshes, carbon storage from kelp forests, and above-ground carbon storage in tropical forests (Tables 1 & 2). Reviewing case studies revealed a key pattern: the species providing these services commonly also form habitats critical to a far broader array of species (e.g., the salt marsh vegetation that provides coastal protection and the mangrove trees contributing to carbon sequestration). Although the service values of carbon storage in kelp forests and mangrove systems may be relatively small compared to the storage benefits of other ecosystems, the key service providers provide critical habitat to a broad array of other species (Steneck *et al.* 2002). Managing for relatively small service values may have broad incidental conservation benefits.

Table 1. A description of the ecosystem services reviewed for part 4.

Ecosystem type	**Ecosystem functions underpinning service**	**Final service**	**Description**
Salt marsh	Wave attenuation & shoreline stabilization	Coastal protection	Avoidance of property damages and injuries from storms provided by coastal ecosystems that reduce storm surge (Barbier *et al.* 2011).
Kelp forest	Carbon storage	Regulation of climate	Kelp primary production can store carbon when kelp biomass is transported to the deep sea (Reed & Brzezinski 2009).
Natural and semi-natural habitat in agricultural landscapes	Pollination from native pollinators	Crop production for food supply	Production of commercial crops benefit from and, in some cases, rely on native pollinators, including watermelon, sunflower, strawberry, muskmelon, tomato, almond, eggplant, cucumber, and squash (Kremen *et al.* 2002a).
Mangroves	Carbon sequestration or "blue carbon"	Regulation of climate	Sequestration of carbon by mangrove ecosystems – estimated to be relatively high compared to sequestration rates in other ecosystems at 226 ± 39 $g\ C/m^{-2}/yr^{-1}$ on average (McLeod *et al* 2011).
Tropical forest	Tree carbon storage	Regulation of climate	Storage of carbon in tropical forests. Here we consider above-ground biomass from trees in natural forests, which account for around half of the carbon storage in some tropical forests (Ngo *et al.* 2013).

Table 2. A summary of ecological drivers and groups of species that provide the services we review.

Ecosystem Service	Ecosystem type	How the service is supplied
Coastal protection	Salt marsh	Vegetation characteristic (plant stiffness and marsh width) contribute to wave attenuation, while species identity, vegetation biomass, and vegetation height correlate with shoreline stabilization (Shepard *et al.* 2011; Paul *et al.* 2012). The value of coastal protection varies with hydrodynamic conditions (Wamsley *et al.* 2010; Shepard *et al.* 2011; Paul *et al.* 2012) and how well vegetation reduces wave energy (reviewed in Pinsky *et al.* 2013).
Carbon storage	Kelp forest	Kelp uptakes carbon during photosynthesis and can store carbon when dead kelp is transported to the deep sea (Harrold *et al.* 1998; Reed & Brzezinski 2009; Wilmers *et al.* 2012; Chung *et al.* 2013). The ability for kelp to contribute to carbon storage depends on both net primary productivity, which translates to biomass production that uptakes C, and the total amount (biomass) of kelp that reaches the deep sea versus decomposes in near-shore environments where much of the carbon is released (Reed & Brzezinski 2009; Wilmers *et al.* 2012).
Carbon sequestration	Mangroves	In mangrove ecosystems, carbon is sequestered in sediment, living (e.g., trees’ leaves, stems, roots) and in non-living biomass (e.g., litter) (Mcleod *et al.* 2011). The depth of organic sediment is responsible for most of total carbon storage (e.g., 49-98% in the Indo-Pacific; Donato *et al* 2011), but mangrove species biomass and benthic fauna responsible for C burial also influence carbon sequestration rates’ along with mangrove forest age, temperature, and local geomorphology (Alongi *et al.* 2004; Mcleod *et al.* 2011).
Pollination of crops	Various habitat types surrounding agricultural	Pollination of crops by native pollinators is a function of the visitation

	land	frequency and the amount of pollen deposition per visit (e.g., grains of pollen deposited by an individual). More common species visit crops more frequently, whereas deposition efficiency varies by species (such as due to differences in body size) (Kremen *et al.* 2002b; Larsen *et al.* 2005; Winfree *et al.* 2007, 2015; Garibaldi *et al.* 2013; Kleijn *et al.* 2015).
Above-ground carbon storage	Tropical forests	The amount of above-ground carbon stored in trees is often calculated as a function of the biomass of the tree stocks (which depends on abundance) and of functional characteristics of the tree species: wood density, size, diameter, life span, and growth rate. The functional characteristics also determine how length of time a tree species stores carbon (Fauset *et al.* 2015).

Managing these ecosystems for service benefits alone could have broad additional conservation benefits for biodiversity at no added costs. With the exception of pollination, habitat-forming species directly provide each service reviewed here (Table 2). Further, to enhance pollination by native pollinators, a primary management action is commonly to restore natural habitat (e.g., hedgerows of native vegetation) near farmlands (Kremen *et al.* 2004; Ricketts *et al.* 2008; Chaplin-Kramer *et al.* 2011). Restoring natural and semi-natural vegetation could also provide broad co-benefits for biodiversity, including vulnerable and specialized species (Kremen & M'Gonigle 2015). Therefore, managing for these regulating services by restoring, protecting, or enhancing the species that provide them will likely have extensive and diverse co-benefits for other species, even when the management goal is not explicitly conservation. This pattern may likely hold for other regulating services (e.g., pest control by native predators, Kremen and Miles 2012).

Discussion, Future Directions, and Conclusions

We identified and reviewed several factors that strengthen the alignment between ecosystem services and conservation and several factors that do not. Broader alignment occurs when rare species play critical roles, if multiple services greatly expand the number of critical species, and likely when longer time horizons are considered. Alignment is also greater when management for ecosystem services and for biodiversity conservation – such as land management and restoration – require the same actions, such as by prioritizing the same locations, habitats, and species (for restoration). In addition, for many regulating services, management focused solely on a single service can provide broad incidental benefits to biodiversity at no added costs via enhancing, restoring, or protecting the habitat-forming species that provide services.

In contrast, several issues could weaken alignment between these objectives. In particular, the conservation benefits from land management for ecosystem services can be considerably lower than if land management focused primarily on conservation (Chan *et al.* 2006; Nelson *et al.* 2009; Polasky *et al.* 2012a). Alignment will also be weaker if many rare species – especially those at greatest risk of functional extinction – never play a role in any service in any of the ecosystems in which they occur. A focus on ecosystem services could therefore remove an economic incentive to protect this class of species most at risk of extirpation.

Much less is known about the role of rare species in service provisioning. While this uncertainty suggests a precautionary approach for ecosystem service management (Ehrlich & Mooney 1983; Lyons *et al.* 2005), identifying and predicting when and under what conditions rare species might be significant contributors would be a fruitful area for future research. Future research could improve understanding about which rare species contribute to services currently or about the potential for rare species to contribute significantly under future environmental and management conditions (e.g., as in Walker *et al.* 1999). Research could also help determine when species switch from rare to dominant, identify factors that drive these fluctuations in species dominance through time and across contexts, and assess whether these potential changes are predictable, such as based on climatic variables. These questions could be addressed in part by using non-random species removal experiments and including threatened or relatively rare species in biodiversity-ecosystem function experiments. However, given the large number and diversity of rare species and logistical constraints of fully factorial experiments, approaches for bioprospecting and optimal search (e.g., Polasky *et al.* 1993, 2005; Costello & Ward 2006) can help researchers decide which or how many rare species to ‘sample’ for a potential role in service provisioning. Future research should also take better advantage of natural experiments (especially with time-series data) that occur at larger scales. Together, this information could refine our knowledge about fraction of species that are or could be critical to services.

In summary, the objectives of conserving biodiversity and delivering ecosystem services align more frequently than would be predicted by considering only the known and direct contributions of abundant species to current ecosystem service provisioning. However, significant uncertainty remains, especially surrounding the service provisioning roles of the vast number of rare species in nearly every ecosystem.

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III. Functional diversity of catch mitigates negative effects of temperature variability on fisheries yields

Abstract

Temperature variation can impact biological processes driving population abundances, with important but unexplored implications for ecosystem services these populations provide, including food production. The impact of temperature variability on yields may depend on the number of harvested species and differences in their responses to varying temperatures. We develop a framework, drawing on thermal performance studies, that predicts that greater temperature variability within years will reduce yields, but harvesting a large number or functionally diverse set of species decreases this impact. We hypothesize that higher functional diversity (FD), measured using traits related to species' responses to temperature, can mitigate impacts from temperature variability on yields. Using a global marine fisheries dataset, we find that within-year temperature variability reduces yields but current FD of targeted species largely offsets this effect, avoiding annual losses of 8% on average globally relative to if FD were degraded to the lowest level observed in the data.

Introduction

Temperature can have substantial effects on populations and their dynamics. The greatest attention has focused on the impacts of projected changes in mean temperatures

(Parmesan & Yohe 2003; Deutsch *et al.* 2008). However, temperature variation within a year is typically far larger than the predicted increases in mean temperature over multiple decades (Helmuth *et al.* 2014, and *references within*). Small changes in temperature can have disproportionately large effects on biological processes such as growth, development, and survival because of the non-linear relationship between these processes and environmental temperature (Angilletta 2006; Deutsch *et al.* 2008; Dell *et al.* 2011; Huey *et al.* 2012; Paaijmans *et al.* 2013, *etc.*). As a result, changing the variability around the mean temperature can dramatically alter rates of these critical processes that affect population dynamics, abundance, and species' distributions (Morris *et al.* 2008; Clusella-Trullas *et al.* 2011; Estay *et al.* 2011, 2014; Vasseur *et al.* 2014). Therefore, shifts in the magnitude and pattern of short-term temperature variation may have greater population effects than long-term warming (Helmuth *et al.* 2014).

An important but underexplored question is whether the effect of within-year temperature variation on populations has consequences for the provision of ecosystem services. Indeed, some services, including food provision from wild harvest of species, depend directly on populations that may be impacted by within-year temperature variation. However, yields will depend on the mix of species being harvested, because species can respond differently to within-year temperature variation. Ecological research and theory suggest that species diversity can raise levels of ecosystem functions (e.g., productivity) in variable environments. For instance, when species compete for resources, differences in their responses to environmental fluctuations can lead to higher overall biomass (Yachi & Loreau 1999; Lehman & Tilman 2000; Ives & Hughes 2002), and communities with more species may be more likely to contain productive or thermally tolerant species (Tilman & Downing 1994). Most theory focuses on inter-annual variability (Yachi & Loreau 1999; Ives & Hughes 2002). Considering within-year variability, Norberg *et al.* (2001) predict that high phenotypic diversity within a functional group results in higher long-term productivity than from any single species. Similarly, the relationship between temperature variability and yields may depend on how much the harvested species differ in their thermal tolerance characteristics. For instance, in a year with highly variable temperatures, sets of species with diverse temperature characteristics may be more likely to contain thermally tolerant species.

Yields from marine fisheries are an important ecosystem service that might be affected by the impacts of temperature variability. Globally, marine fisheries provide employment, billions of dollars in income, and over 79-million tonnes of protein annually (FAO 2010; Sumaila *et al.* 2011). Variation in sea surface temperature has been suggested to significantly impact fisheries yields (Brander 2007, 2010; Cheung *et al.* 2010), but most previous studies focus on long-term trends (warming) and multi-year and decadal oscillations (e.g., ENSO) rather than within-year variation (e.g., Overland *et al.* 2010; Sumaila *et al.* 2011; Doney *et al.* 2012). However, short-term temperature variability may also be an important driver of fisheries yields, as many fish are sensitive to these shorter-term fluctuations (Roessig *et al.* 2004, and *references within*).

Here we use theory on species' responses to temperature changes to **1)** generate predictions about how within-year temperature variability will influence yields and **2)** explore how diversity of species and their traits can alter this relationship. The framework predicts that, for species adapted to the mean temperature in an ecosystem, greater variability within years should reduce yields, but that the diversity of harvested species can mitigate these effects. We empirically test these hypotheses using a global dataset of marine fisheries yields.

Theoretical framework

We aim to understand the relationships among temperature variability, diversity, and service provision. We extend existing theory on thermal performance curves (TPCs) to model the effects of within-year temperature variation on yields. TPCs show how growth rates (r) in ectotherms depend on environmental temperature (T) (e.g., Amarasekare & Savage 2012; Estay *et al.* 2014). Empirical work shows that per capita intrinsic growth rates respond non-linearly to changes in temperature, meaning $r(T)$ [i.e. the TPC] is non-linear (Deutsch *et al.* 2008; Neuheimer *et al.* 2011; Vasseur *et al.* 2014). We use TPCs to model direct responses of growth rates to temperature variation (Fig. 1). To examine the consequences for annual yields, we model population harvest of a single species, extending a standard Gordon-Schaeffer model. Our extension explicitly includes how temperature impacts per capita growth rates, which in turn impact annual yields via biomass available to harvest (Appendix S1). Finally, we consider the harvest of multiple species, which may differ in their TPCs, to explore the role that diversity may play in determining the impacts of temperature variability on aggregate yields.

Harvest of a single species

First, we model how within-year temperature variability may impact yield from a single species. We consider a population of size $X(t)$ at time t that grows logistically under variable temperatures during a growth period τ, with a carrying capacity K and intrinsic growth rate r. Then it is harvested instantaneously at the end of the year (at $t = \tau$). The key feature of our model is that the growth rate $r(T)$ depends on temperature T. Because temperature varies with time $T(t)$, growth rate is written as $r(T(t))$, and we can model population change through time including the effect of variable temperature via the growth rate as

$$\frac{dX}{dt} = r\big(T(t)\big)X(t)\left(1 - \frac{X(t)}{K}\right). \tag{1}$$

The growth rate r plays a crucial role in determining a population's dynamics and its ability to support harvest. In particular, r is proportional to the largest level at which an exploited species can be harvested sustainably (its maximum sustainable yield). This growth rate also incorporates the effects of several demographic parameters that are difficult to observe in wild populations (e.g., fecundity, survival). The carrying capacity K may also vary with temperature, which could be important for lightly harvested species. However, well over half of global fisheries are overfished or recovering from overfishing (Worm *et al.* 2009), so that $X \ll K$ and density dependence is relatively unimportant. Thus, we focus our attention on the temperature dependence of r.

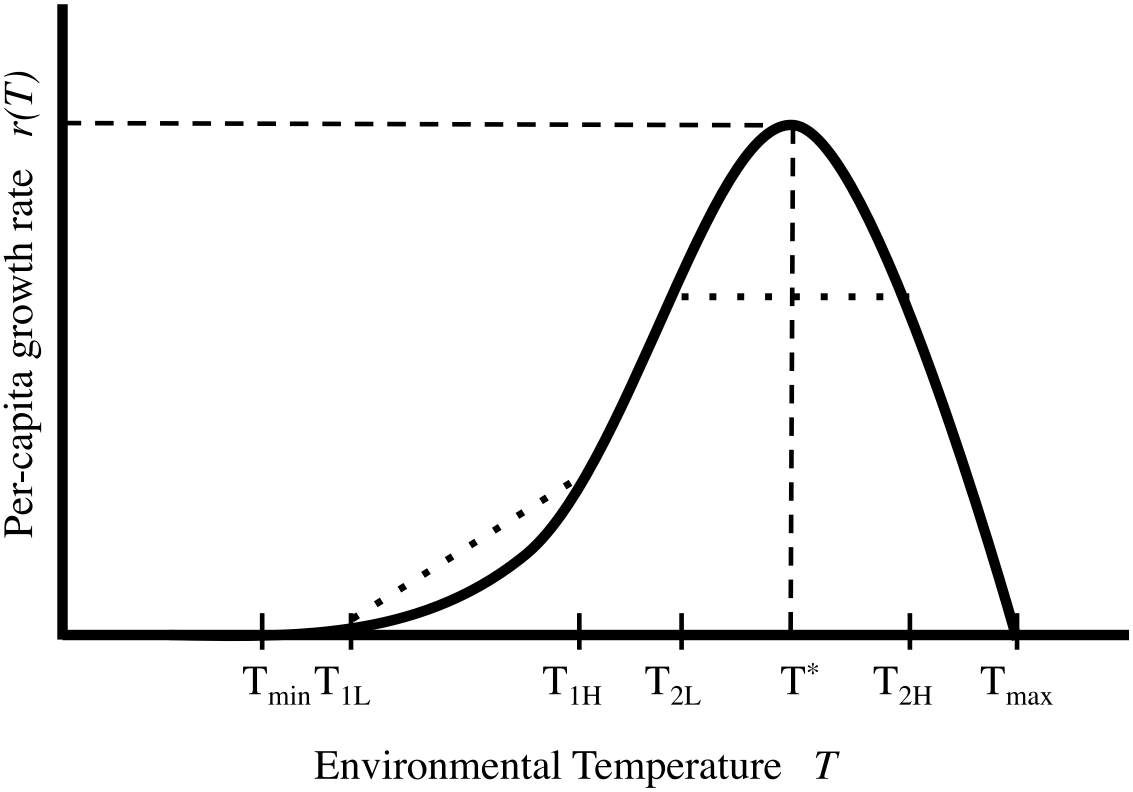
After a growth period of τ, harvest produces yields $y = qEX(\tau)$, where q is a harvest productivity parameter, and E is harvesting effort. Using our population model (1), harvesting the population after allowing it to grow from time 0 to time τ yields

$$y = \frac{qEX(0)e^{\bar{r}\tau}}{1+\frac{X(0)}{K}(e^{\bar{r}\tau}-1)}, \tag{2}$$

where $\bar{r}$ represents the average value of $r(T(t))$ between time 0 and τ (building on work by Quinn & Deriso (1999), see Appendix S1). Though variable temperature results in variable growth rates, the only effect of variable temperature on yield occurs through the average growth rate in this model due to the assumption that harvesting occurs at the end of the growth period τ (i.e., when $t = \tau$). This average growth rate, determined by how much temperature varies during the growth period, is important for yields: we show that yield y is non-decreasing in the average growth rate $\bar{r}$ in Appendix S1, consistent with related models (e.g., Lleonart & Merino 2010).

The effect of temperature variability on yield depends upon how that variability impacts average growth (Appendix S1), which depends on the shape of $r(T)$ (the species' TPC) over the range of realized temperatures. In line with numerous empirical studies on TPCs (e.g., Deutsch *et al.* 2008; Neuheimer *et al.* 2011), we assume $r(T)$ is maximized at an optimal temperature (T^*) and declines to zero beyond upper and lower critical temperature limits, T_{max} and T_{min} respectively (Fig. 1). A species' thermal tolerance is related to the curve's width: species with wider TPCs are more thermally tolerant. Although the shape of TPCs will vary among species, populations, and life stages, TPCs are generally considered to have a steep, negative drop-off in performance above optimal temperatures until the maximum temperature is exceeded, but exponential gains in performance at lower temperatures (Fig. 1) (Angilletta 2006; Dell *et al.* 2011; Amarasekare & Savage 2012).

Figure 1. A conceptual figure of how temperature variability affects intrinsic per capita growth rate (r). Based on thermal performance curves (TPCs), an individual of a species has a temperature optimum (T^*) at which its performance (here growth rate) is the highest, as well as a maximum temperature (T^{max}) above which it does not grow. In the absence of variability, in an environment with constant temperature at T^*, the species maximizes its r. Temperature variability may increase (between T_{1L} and T_{1H}) or decrease (between T_{2L} and T_{2H}) average growth rate, and thus yields, as compared to a constant temperature regime (see "Theoretical framework" section). Depressed growth is more likely for species adapted to their average ecosystem temperature, i.e. $T^* \approx \bar{T}$. Dotted lines represent average growth rates in variable temperature regimes featuring both low and high temperatures; the relative frequency of those temperatures determines location of the dotted line.



How temperature variability impacts average growth depends on the curvature of the TPC over the range of temperatures that a species experiences (the realized temperatures) (Fig. 1). Increased temperature variability widens the ranges of realized temperatures. If a TPC is concave over the range of realized temperatures, then by Jensen's inequality, the average growth rate in the variable temperature regime ($\bar{r} = \overline{r(T)}$) is smaller than the growth rate at a constant (average) temperature, $r(\bar{T})$. The opposite is true if the TPC is convex: temperature variability will increase the average growth rate. If the range of temperatures encompasses both convex and concave regions of the TPC, the net effect is indeterminate. However, in general, temperature variability will have a nonzero effect on average growth $\bar{r}$ (consistent with Bozinovic *et al.* 2011; Estay *et al.* 2014) and thus a nonzero effect on yield.

Most importantly, our model predicts that for species that are adapted to the average temperature $\bar{T}$ in an ecosystem such that T^* is close to $\bar{T}$, variation in temperature is likely to span a concave region of the TPC, so temperature variability will have a negative effect on yields.

Harvest of multiple species

Previous research in other systems suggests several reasons why diversity in the number of species and/or in their characteristics could mediate the impacts of temperature variability on yields. First, harvesting more species (greater species richness) increases the likelihood of catching a species that is more tolerant to variation. The average growth rate of a more tolerant species will be less affected by variation, which can help buffer decreases in average growth when variability is higher, or compensate if species compete (Tilman & Downing 1994). Therefore harvesting more species could potentially decrease the impact of temperature variation on total harvest.

The effect of diversity could also be driven by differences in the characteristics of species' TPCs, regardless of the number of species harvested. For species adapted to the average temperature in an ecosystem, variability negatively affects average growth and thus yield. Harvesting a more diverse set of species by including species with different optimal temperatures may result in some species being positively impacted by variability, thereby increasing aggregate yield (Fig. 2). In addition, resource-competition models suggest that diversity in the location of optima can result in higher overall community biomass because of greater "coverage" of possible environmental conditions (Lehman & Tilman 2000; Ives & Hughes 2002). Diversity in optima could arise, for example, because no one species can be best for all temperatures when temperature varies, so many species can evolve and coexist. Other theory suggests that when species respond asynchronously to environmental fluctuations, this negative covariance can increase average biomass of a community (Yachi & Loreau 1999). We suggest that differences in species' TPCs could be one mechanistic reason why species' biomasses respond asynchronously to temperature fluctuations, resulting in higher yield. If all harvested species have the same TPC shape, their responses to temperature will be perfectly positively correlated, and diversity would have no effect on yields (following Yachi & Loreau 1999).

Figure 2. Effects of temperature variability on growth rates of multiple species as represented by Thermal Performance Curves, or TPCs (solid lines). In a low (zero) variability regime, species A has higher average growth. In high variability regimes (e.g. temperatures T_L and T_H occur), species B has higher average growth (dotted lines). Harvesting a pool of species with more diverse TPCs is likely to include more species like B, increasing average growth (and thus yield) under variable temperature conditions. Dotted lines represent average growth rates in variable temperature regimes featuring both low and high temperatures; the relative frequency of those temperatures determines location of the dotted line.

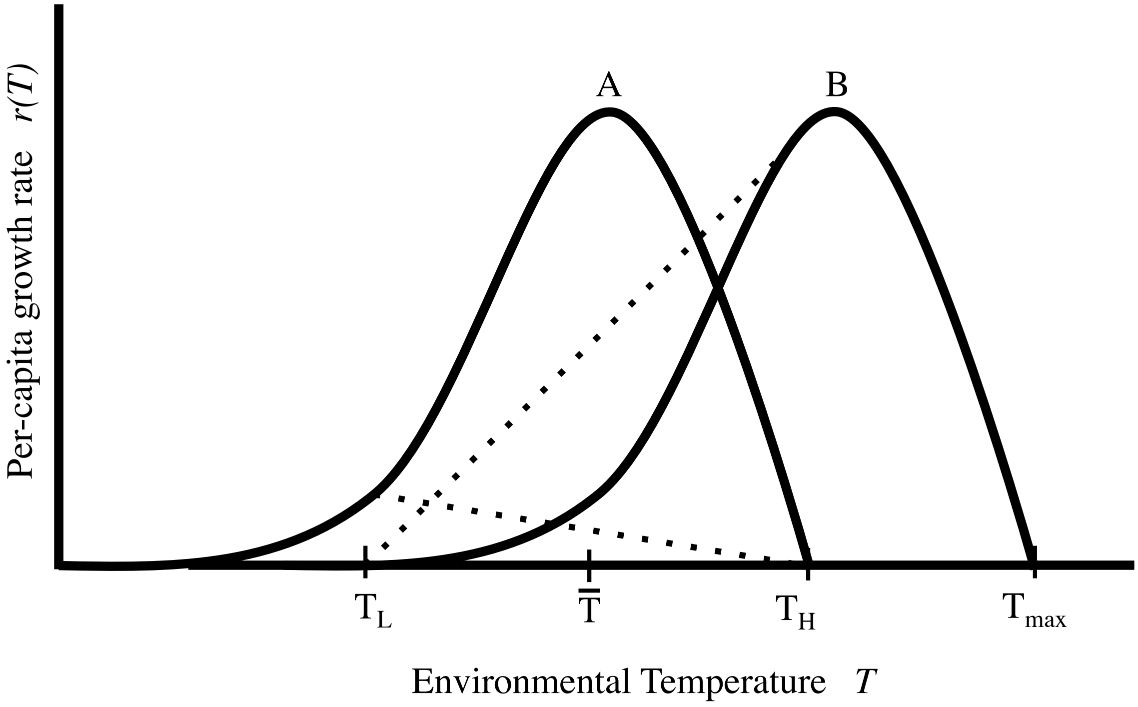
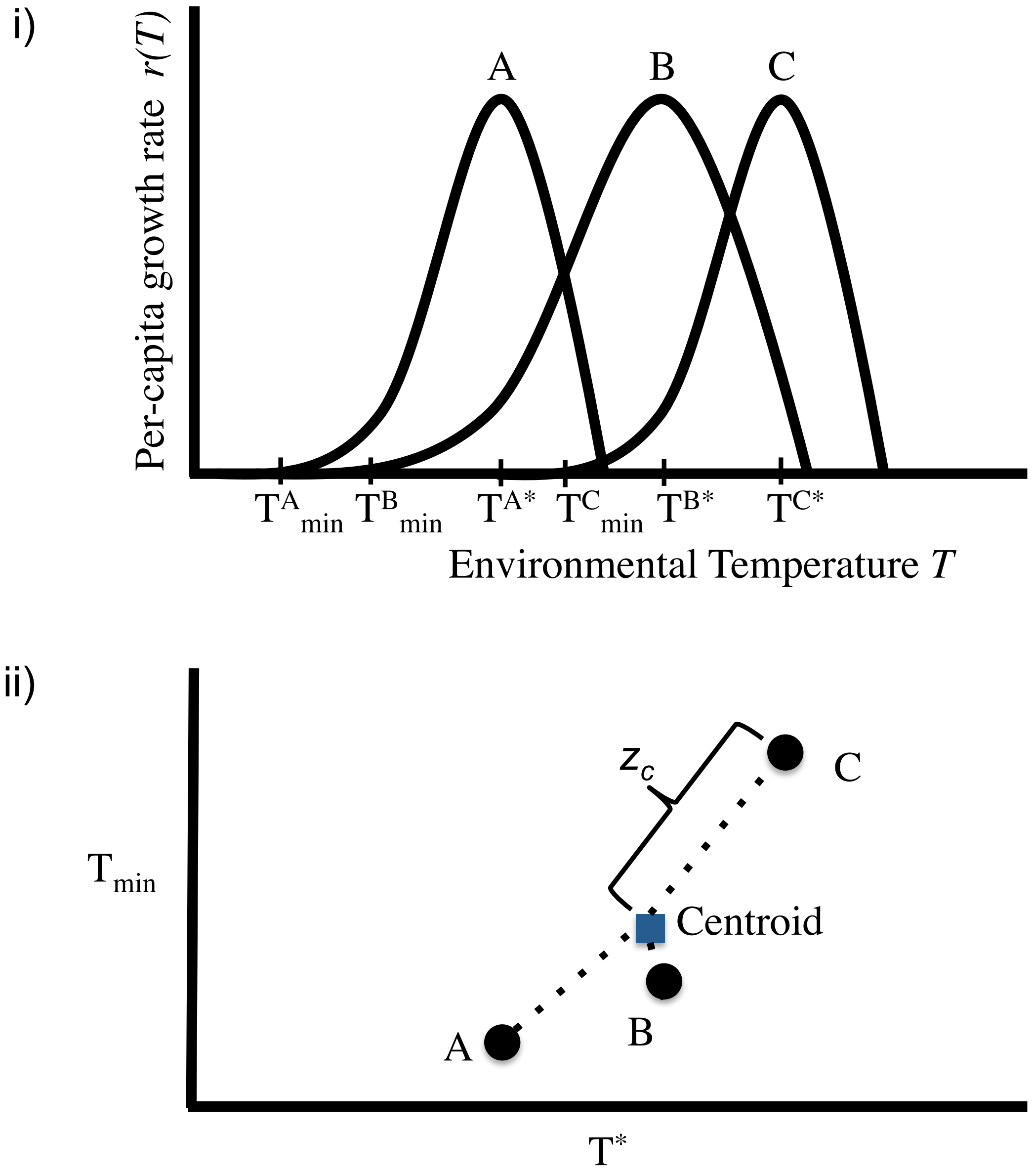


Figure 3. A conceptual figure of how characteristics of thermal performance curves (TPCs) of multiple species could be measured by functional diversity, here measured as Functional Dispersion. ***i***) shows that Species A, B, and C differ in their temperature optima (T*) and range, i.e., minima (T_{min}) and maxima (T_{max}). ***ii***) shows how these parameters, which determine the shape of a species' TPC, can be interpreted as 'traits' that characterize a species' response to temperature fluctuations. These traits, or proxies for them, can be used to compute the functional dispersion of the set of species, which we illustrate with T* and T_{min}. Functional dispersion measures the mean distance (Z_i) between a hypothetical "average" or "centroid" species and each species in the community. Our empirical analyses use maximum depth and habitat association as proxies for T_{min} and T^* respectively, as they are highly correlated with temperature range.



In our empirical analysis of fisheries, we employ measures of functional diversity (FD) to capture differing responses to temperature variability (Fig. 3). In contrast to species richness, which treats species as functionally identical, FD measures differences between species, often based on the values of particular traits (Díaz & Cabido 2001; Petchey & Gaston 2006; Cadotte *et al.* 2011; Tilman *et al.* 2012). FD can be measured in many ways, depending on the metric choice and traits included (reviewed in Mouchet *et al.* 2010). Here, FD focuses on differences in thermal performance curves, meaning $r(T)$ differs by species (i.e., different temperature tolerances, optima, or critical limits) (Fig. 3). Given that we are interested in the effects of temperature variation, we predict that measuring diversity in thermal performance characteristics (or proxies for them) is likely to be a more informative measure of diversity than species richness.

Empirical Analysis: Methods

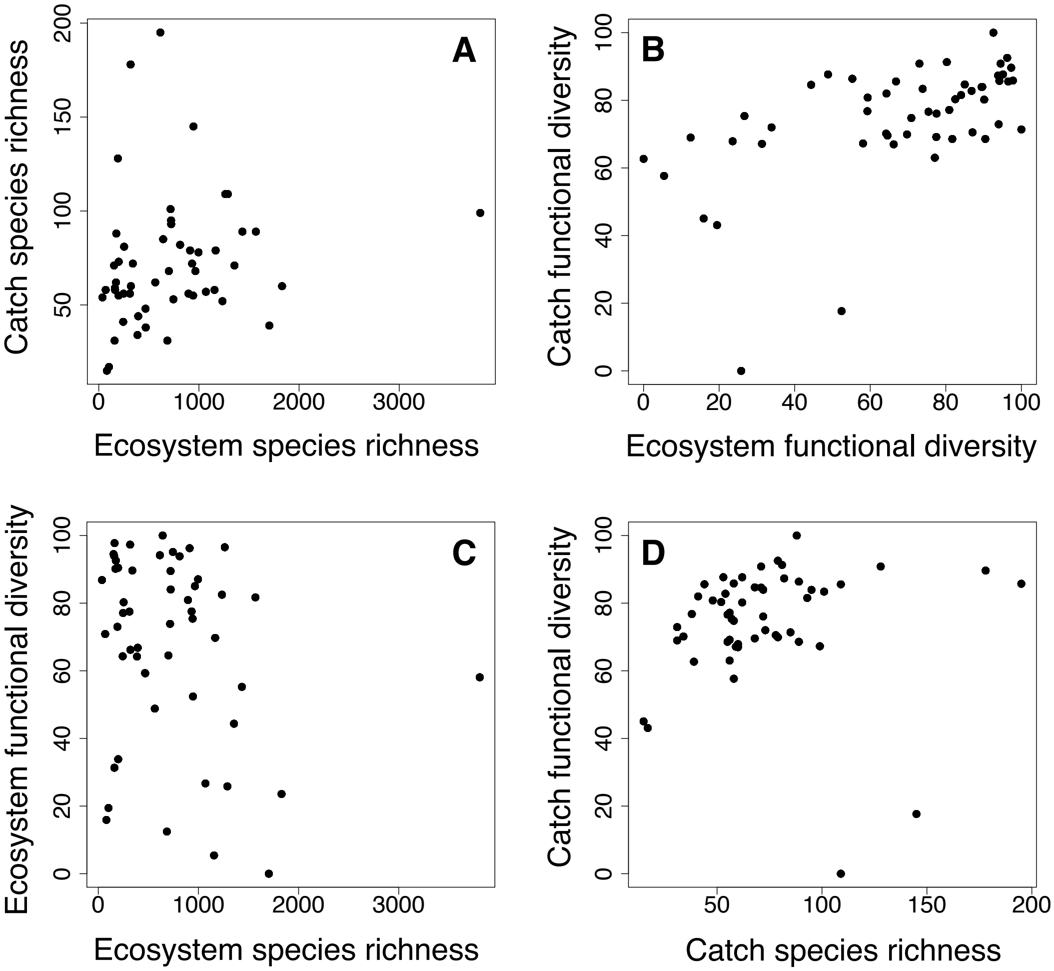
The preceding framework suggests that temperature variability will decrease yields of species and that harvesting a larger number of species or species with more diverse TPC characteristics will decrease the negative impact of temperature changes on total harvest, provided not all species are optimally adapted to the mean temperature. We next test these predictions with a global fisheries dataset asking: 1) does within-year temperature variability impact the annual levels of global fisheries yields? and 2) if so, can species richness and/or functional diversity mediate the effects of this temperature variability on aggregate yields? We hypothesize that FD of the harvested species, measured in terms of traits that reflect TPCs (Fig. 3), can mediate the effect of temperature variability on total yields.

We estimate models of total annual fisheries yield from 1982-2006 in 53 distinct ocean regions. These ocean regions, referred to as Large Marine Ecosystems (LMEs), delineate areas spanning from the coast to the edge of the continental shelf based on shared ecological and hydrodynamic characteristics (Sherman & Hempel 2009). Specifically, we model total yields in an LME and year as a function of within-year temperature variability, its interaction with biodiversity, and other factors known or posited to influence fisheries yields (Appendix S2 and Table S1 describe the dataset). While our analysis focuses on estimating the direct effect of within-year temperature variability and its interaction with biodiversity on yields, it is worth noting why we do not estimate a main effect of biodiversity on yields. Total yields may vary dramatically across LMEs for many confounding reasons other than diversity, including baseline differences in productivity, LME size, mean species' length, and the probability of fishing sustainability (factors shown to be important in Chassot *et al.* 2010; Fisher *et al.* 2010). To control for these baseline differences in LMEs as well as unobservable drivers of yields, we absorb all time-invariant differences between LMEs into per-LME intercepts. Per-LME intercepts also absorb the direct effect of diversity on yields because our measures of biodiversity are time-invariant.

We estimate the direct effect of within-year temperature variability on yields. Within-year variability of sea surface temperature (SST) is measured for each year by the coefficient of variation (CV) of monthly temperatures for each 1°x1° spatial cell, averaged across all cells in an LME (using NOAA 2014 data). We test the robustness of results using the standard deviation of SST, another measure of within-year temperature variability (Appendix S2). We focus on CV as our measure of variability because the width of TPCs likely scales with the mean temperature (which is incorporated into the CV measure).

The defining part of the models is the interaction term between temperature variability and biodiversity. It allows the effect of temperature fluctuations on fisheries yield to depend on the level of biodiversity, testing whether and how biodiversity mediates the impacts of temperature variability. We consider several metrics of biodiversity, including taxonomic (species richness, or SR) and functional metrics (functional diversity, or FD, here measured as functional dispersion, *sensu* Laliberté & Legendre 2010) (for an explanation see Fig. 3). For both SR and FD, we measure the diversity of both the targeted species and all fish species in each LME (Fig. 4; Table S1). We measure functional dispersion with respect to traits that act as proxies for species' temperature preferences due to poor global coverage in species' temperature minima and maxima information (Figs. 3 & 4, Appendix S2; Froese & Pauly 2012). Specifically, we use habitat associations and maximum depth traits, because depth range maximum is highly correlated with temperature traits, and all habitat types are significant predictors of temperature traits (Appendix S2). Maximum depth is a good proxy for $T_{min,}$ and habitat association is likely associated with T* (consistent with Clusella-Trullas *et al.* 2011). Functional dispersion computed with different traits contains different information (Fig. S2), so we also examine the importance of trait selection. To construct a falsification test, we include a measure of FD based on traits that we would not expect *a priori* to influence responses to temperature variation in the current year (tropic level and trophic level of diet) (Appendix S2). FD metrics are scaled between 0-100.

Figure 4. The relationship between the diversity of the catch versus the ecosystem (all fish) and different diversity metrics, species richness (SR) versus functional diversity (FD), for the 53 Large Marine Ecosystems in the analysis. FD scores were scaled between 0-100. **A)** SR of the ecosystem versus of the targeted species are not meaningfully correlated (*r* = 0.191). **B)** FD metrics calculated for the ecosystem versus the targeted species are not highly collinear (*r* = 0.556). **C)** Relationship between SR and FD of the fish in the ecosystem (*r* = -0.204). **D)** SR versus FD of the targeted species (*r* = 0.072).



We estimate models of the form

$$\log(Y_{it}) = \propto_i + P_i(t) + \beta_T V(T_{it}) + \beta_{BD} V(T_{it}) \cdot BD_i + \gamma X_{it} + \varepsilon_{it} \qquad \textbf{(3)}$$

where Y_{it} is total yield in LME i in year t, $V(T_{it})$ represents within-year temperature variability, BD_i is a vector of the biodiversity metrics, X_{it} is a vector of other explanatory variables, and ε_{it} is an error term. The other explanatory variables include number and presence/absence of individual quota programs (Environmental Defense Fund 2012) and of Marine Protected Areas (Wood 2007), number of stock assessments as a proxy for scientific robustness (Ricard *et al.* 2012), and upwelling potential (mean minus minimum SST, Appendix S2). There are many other factors that differ across locations and time that affect historical yields but lack robust data at a global scale (e.g., economic development, fisheries expansion, and other inherent difference in ecosystems and the species within them). Controlling for these factors is important so that their effects on annual yields over time are not misattributed to temperature variation and diversity. We control for these unobserved differences across LMEs through an intercept per LME $\propto_i$ (time-invariant) and per-LME polynomial time trends $P_i(t)$. The per-LME intercepts account for baseline differences in LMEs, while the per-LME time trends account for gradual changes in fishing effort, capacity, and management through time – important factors for fisheries yields that vary through time but lack available time-series data. Per-LME polynomials, including a linear trend, also control for effects of smooth trends in mean SST on yield (e.g., from ocean warming).

From equation (3), the effect of an increase in temperature variability on catch will depend upon biodiversity:

$$\frac{\partial \log(Y_{it})}{\partial V(T_{it})} = \frac{\partial Y_{it}/Y_{it}}{\partial V(T_{it})} = \beta_T + \beta_{BD} \cdot BD_i. \quad \textbf{(4)}$$

The signs of β_T and each coefficient estimate of β_{BD} will determine whether the corresponding type of biodiversity dampens or magnifies the effect of an increase in temperature variability on catch. Coefficients of β_{BD} with a sign opposite to β_T indicate dampening effects.

We examined the robustness of our results through alternative model specifications, including alternate time trends, indicators of upwelling (ocean productivity), and lagged variability. Appendix S2 provides details on the robustness checks, dataset, calculations of FD metrics, and model selection. After performing robustness checks and selecting a model, we calculate and interpret the marginal effects of the variables of interest from the preferred model.

Results

Table 1. Results from a linear regression model for log of total annual fisheries yields (in tonnes) by Large Marine Ecosystem (LME) from 1982-2006. The coefficients of interest, for which we test our main hypotheses, are significant ($p < 0.05$) and highlighted in bold. This model specification (of the form from equation 3) includes a per-LME cubic time trend and per-LME intercept (estimates not presented for space reasons). The model uses clustered robust standard errors.

	Estimate	Std. error	t-value	p-value
Upwelling potential	0.0002	0.055	0.004	0.9967
SST CV	**-113.50**	**52.20**	**-2.17**	**0.03**
MPAs (yes/no)	-0.27	0.30	-0.88	0.38
(log) No. MPAs*	0.03	0.08	0.41	0.68
(log) No. Stock assessments	-0.15	0.12	-1.21	0.23
IQs[†] (yes/no)	0.22	0.08	2.59	0.01
No. IQs	0.05	0.04	-1.25	0.21
SST CV : (log) Temperature FD[‡] catch	**21.77**	**5.50**	**3.96**	**<0.001**
SST CV : (log) Species richness catch	24.26	19.57	1.24	0.22

SST CV : (log) Temperature FD all fish	-26.39	15.89	-1.66	0.10
SST CV : (log) Species richness all fish	4.43	8.95	0.49	0.62

F(222 and 1102) = 891.2; R^2=0.993; residual std. error = 0.159; p<0.001
BIC: 250.8147   AIC: -911.5589

**MPAs = Marine Protected Areas*
† IQs = Individual quota programs
‡ FD = Functional Diversity

Testing hypotheses

Within-year temperature variation significantly and negatively affects annual, total yields within an LME, consistent with our hypotheses (Table 1). Similarly, we found strong evidence that FD of the set of harvested species can mediate the negative impacts of within-year temperature variability on yields (Table 1; $\beta_{FDcatch}$ = 21.77, p = <0.001), holding SR constant. In contrast, we did not find strong evidence that SR of the catch had a significant effect. This finding is consistent with Fig. 4, which shows that SR and FD metrics contain different information. Further, the effect of FD depended on which traits were included; FD with traits that are relevant to temperature fluctuations (Table S2) had a significant effect while FD with traits with no *a priori* expectation to determine species' responses to temperature fluxes did not (Fig. S2; Table S2). None of the alternate model specifications substantively alter the results or coefficient estimates of interest; in fact, the coefficient estimates of interest were consistent across model specifications (Table S3).

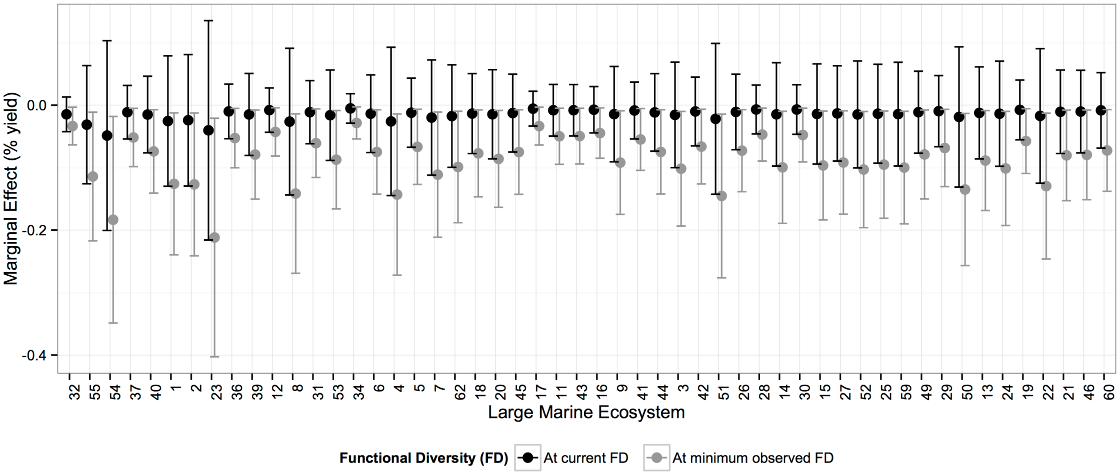
In contrast to FD of the catch, FD of the ecosystem when interacted with temperature variability had a negative and weakly significant effect (Table 1;

β_{FDe} = -26.39, p = 0.10). This effect also depended on computing FD with traits that relate to temperature (Fig. S2; Table S2). We did not find evidence that SR of the ecosystem had effects significantly different than zero in any model (Tables 1; S3).

Interpreting the mitigating effect of catch FD

The FD of targeted species can offset the negative effects of current levels of temperature variability (Fig. 5). However, if FD were degraded in every LME to that of the LME with the lowest observed FD of targeted species in the dataset, the loss to harvest would be on average 8% of global yields, or an average of 85,000 tonnes per LME and year under current levels of temperature variability (Fig. 5; Table S4). All LMEs experience a loss in yields given this reduction in FD of targeted species. On average, our results suggest that the Humboldt Current would experience the largest absolute loss in yields: -760,000 tonnes per year (95% C.I. = +/- 350,000 tonnes; 9% loss) of an average of 8,500,000 tonnes per year (based on 1982-2006). The Beaufort Sea would have the smallest reduction in yields (-33 tonnes per year; 95% C.I. = +/- 15 tonnes; 12% loss) out of an average of 280 tonnes per year. For other LMEs, the magnitude of these effects will depend on the levels of historical temperature variability and functional diversity of the targeted species, which vary by region (Table S4). Note that the reported losses in yield assume the estimated marginal relationships hold over a large range of functional diversity and therefore should be treated as approximations only.

Figure 5. Marginal effects of temperature variability on fisheries yield per LME at current levels of catch functional diversity (FD, black) and at the lowest level of catch functional diversity observed in our dataset (gray), which was in the Red Sea Large Marine Ecosystem. Catch functional diversity here is measured using the temperature-related trait set. Effects reported as percent change in yield. Error bars indicate 95% confidence intervals. The magnitudes of these marginal effects for each Large Marine Ecosystem are presented in the supplemental materials (Table S4). The Large Marine Ecosystems are ordered from least functionally diverse to most functionally diverse (in terms of temperature traits), from left to right.



Discussion

This study fills an important research gap by jointly considering ecosystem services, biodiversity, and thermal performance in the face of variable temperatures over short time scales. Connecting these sub-disciplines provides new insights about the consequences of temperature variation for yields and the role of diversity in mediating this relationship. Our theory links thermal performance curves (TPCs) and temperature variability to their consequences for provisioning services based on harvest of ectotherm populations. Further, we identify a pathway through which diversity could influence aggregate yields in the face of within-year temperature variability.

As hypothesized, higher temperature variability within a year negatively impacts average yields; however, the magnitude of this impact is smaller in regions with greater functional diversity (FD) of targeted species. Specifically, our analyses provide evidence that FD in traits that act as proxies for species' TPCs can mitigate effects of within-year SST variation on total yields, after controlling for SR (Fig. 4). This result suggests that during more variable years -- or if within-year temperature variability increases in the future -- FD in thermal characteristics of targeted species could be even more important.

Our empirical results reveal several advantages to a hypothesis-driven approach when testing for effects of biodiversity on ecosystem services. First, the effects of biodiversity on yields depend heavily upon how diversity is measured and for what collection of species (Fig. 2). Of the metrics considered, only the FD of the target species – measured with traits related to TPCs – consistently had a significant and positive interaction with within-year temperature variability (Tables 1, S2 & S3). In contrast, FD of the ecosystem (of all fish species) compounded the negative effect of temperature variability (Table 1). One explanation for this result is that increasing FD of non-targeted species could allow non-target species to outcompete target species for resources under more variable conditions. Further, FD of the target species only mediated temperature variability effects if measured with traits related to their potential responses to temperature (Table S2), corroborating our interpretation of the results. Together, these results highlight the importance of clearly defining the type of and the pathway through which biodiversity may influence services like fisheries.

Testing the hypothesis that biodiversity mediates how temperature variability impacts aggregate fisheries yields differs from prior work on biodiversity and global fisheries. Specifically, previous studies examine a reduced-form relationship (‘main effect’) between biodiversity and global yields and only use measures of SR (not FD). Worm *et al.* (2006) and Chassot *et al.* (2010) estimated the effect of ecosystem SR on measures of aggregate yields. While Worm *et al.* (2006) found that ecosystem SR was positively correlated with average yields of non-collapsed stocks, Chassot *et al.* (2010) found no evidence that SR of the ecosystem contributed to productivity of yields. We also found no evidence that SR of the ecosystem offsets negative impacts of within-year temperature variability. Further, Worm *et al.* (2006) concluded that the SR of the catch had a positive correlation with total production of catch, whereas we did not find consistent evidence that SR reduced the negative impacts of within-year temperature variability on total, annual yields (yields summed across harvested species) (Table S3). Importantly, these results are not incompatible: the SR of the catch could impact aggregate yields through a mechanism other than by reducing the impact of temperature variability.

We examined the effects of within-year temperature variability on growth and yields, but longer-term temperature changes may also impact yields both directly and in interaction with shorter-term variability (Estay *et al.* 2014; Vasseur *et al.* 2014). While our empirical approach is designed to control for long-term (smooth) trends, it does not study those trends directly. Evidence shows that increases in mean SST are already impacting species by reducing growth rates when a species’ maximum temperature is exceeded (Neuheimer *et al.* 2011), shifting distributions of stocks (Perry *et al.* 2005), and redistributing the location of their yields (Cheung *et al.* 2013). Yet, many of these studies did not directly address the interaction between mean temperature and variation, and, as the climate changes, the effects of changing temperature variability may depend upon the shifts in mean temperature and *vice versa* (Bozinovic *et al.* 2011; Vasseur *et al.* 2014). Similarly, interactions between changes in the mean and variance of temperature may also be important for the relationship between diversity, temperature, and yields, especially when these shifts favor the growth and production of different species. Forecasting the consequences of climate change, and estimating other ways that diversity may be important, will require a better understanding of how within-year variation couples to longer-term variation and trends in temperature.

While our results identify a potential link among temperature variability, biodiversity and fisheries yields, further research is needed to elucidate the underlying mechanism(s). Sampling effects, differences in temperature optima, or fishers altering their harvesting behavior to take advantage of differences in species' productivity under different temperature regimes (discussed below) could all lead to the observed result that more functionally diverse portfolios of target species decrease the negative effects of temperature variability on total yields. Further theoretical analyses could identify approaches to distinguish among these different mechanisms via signals that are measurable at management-relevant scales in observational datasets.

Similarly, our theory focused on how temperature variability directly impacts intrinsic growth rates, which encompasses many biological processes. Future modeling work could tease apart the effects of temperature variability on survival, biomass growth, fecundity, and carrying capacities. Temperature variability could also indirectly affect growth rates and therefore yields, such as by altering primary productivity and food web dynamics. Our empirical analyses control for changes in mean and time-varying differences in productivity (with per-LME intercepts and upwelling potential), but the theory does not explicitly consider these indirect pathways. The indirect effects of temperature variation on fisheries yields, such as via predator-prey interactions, merit future investigation. For instance**,** the net effect of temperature variation on the fisheries species could be positive if its prey does better under a more variable temperature regime. Therefore, the net effect of short-term variation on population dynamics and yields may be a fruitful area for future research (especially when species interact).

Human behavior could also provide an explanation for the positive effect of catch FD on yield in that more diverse sets of species enable fishers to target a species better suited to the current temperature regime, either actively or passively. Anecdotally, fishers actively shift effort to different fisheries or fishing locations in response to which stocks are most productive under a given temperature regime (Pinsky & Fogarty 2012). Fishers using non-selective gear like trawl nets would passively benefit from thermal FD by capturing the most productive species for a given regime. Such fishing behaviors could be contributing to the observed positive interaction between catch FD and temperature variability.

Managers could actively buffer yields in the face of seasonal temperature variability by intentionally targeting a portfolio of species with diverse thermal performance characteristics. However, many management rules ignore both temperature variability and functional diversity, suggesting great scope for improvement in management. For example, management institutions could alter catch limits (quota) of stocks based on observations of temperature regimes or control how harvesters dynamically reallocate their effort to different species depending on the environmental conditions. Therefore, even under current levels of within-year variability, our findings have potentially important implications for management of services such as fisheries.

How our results will translate to other ecosystem services and their management is a promising area of future research. Other provisioning services driven by year-to-year growth of ectotherms may exhibit similar responsiveness to within-year temperature variability. In contrast, services provided by species with less temperature sensitivity, or which depend upon overall biomass rather than growth (e.g. shoreline protection, ecotourism), may exhibit quite different responses to short-term variability. Further, some populations are highly mobile and can move to thermally optimal parts of the species' range; therefore, this effect of functional diversity may not be seen at smaller spatial scales (i.e., within LMEs) when yields are redistributed as a result of temperature-dependent movement patterns for some species. More empirical research across a variety of systems, spatial scales, and services is necessary to better understand both the effects of short-term temperature variability on the provisioning of ecosystem services and the role that diversity may play in modifying any impacts.

Conclusions

Understanding how climate impacts populations and the ecosystem services they provide is a key research area at the nexus of ecology and climate science. Our analyses suggest that within-year temperature variability has a negative impact on global fisheries yields, but that functional diversity of the harvested species helps mitigate this impact. Despite the potential importance of variability for populations and communities, most natural resource management does not include such considerations, especially the effects of short-term variation. Based on our findings, management strategies that take advantage of functional diversity to help enhance and protect ecosystem service provisioning, such as encouraging fishers to hold permits for diverse stocks, could maintain more productive services into the future. Given that environmental variability is predicted to change in many places as our climate changes (Easterling *et al.* 2000), there is a need for scientists and managers to place more emphasis on understanding the effects of short-term variability on the provisioning of ecosystem services.

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Appendix for Functional diversity of catch mitigates negative effects of temperature variability on fisheries yields

Appendix S1: Theory relating temperature variability to yields

Derivation of yield (Equation 2)

As stated in the text, we assume yield is $y = qEX(\tau)$, where q is a harvest productivity parameter, E is harvesting effort, X is the biomass of a species at the end of its growth period, and τ is the duration of the growth period. Therefore, to determine yield, we need to determine biomass at the end of the growth period $X(\tau)$. Quinn and Deriso (1998) show that integrating the differential equation (1), with a growth rate $r(T(t))$ that varies with time due to its dependence on time-varying temperature, from 0 to τ gives

$$X(\tau) = X(0)\frac{e^{\bar{r}\tau}}{1+\frac{X(0)}{K}(e^{\bar{r}\tau}-1)}, \qquad \textbf{(SI.1)}$$

where $X(0)$ is the starting biomass at time 0. As a result, the biomass available for harvest after growth under time-varying r for a period of duration τ depends only on the average growth rate during that period, $\bar{r}$. Equation (2) in the main text is obtained by simply substituting for $X(\tau)$ from (SI.1) into $y = qEX(\tau)$.

Dependence of yield on average growth rate

Here we show that yield depends positively on the average growth rate, $\bar{r}$, which depends on temperature variability. Partial differentiation of the yield equation (SI.1) with respect to $\bar{r}$ using the quotient rule gives

$$\frac{\partial y}{\partial \bar{\bar{r}}} = qEX(0)\frac{\left[\tau e^{\bar{r}\tau}\right]\left[1+\frac{X(0)}{K}(e^{\bar{r}\tau}-1)\right] - \left[e^{\bar{r}\tau}\right]\left[\frac{X(0)}{K}\tau e^{\bar{r}\tau}\right]}{\left[1+\frac{X(0)}{K}(e^{\bar{r}\tau}-1)\right]^2}. \qquad \textbf{(SI.2)}$$

Simplifying this expression via algebra gives

$$\frac{\partial y}{\partial \bar{\bar{r}}} = qEX(0)\frac{\tau e^{\bar{r}\tau}\left(1-\frac{X(0)}{K}\right)}{\left[1+\frac{X(0)}{K}(e^{\bar{r}\tau}-1)\right]^2}. \qquad \textbf{(SI.3)}$$

Note that q and E are assumed to be positive, *X(0)* is non-negative, and the denominator is clearly positive. For $X(0) \leq K$, all terms in the numerator are non-negative, so that $\frac{\partial y}{\partial \bar{\bar{r}}} \geq 0$, with the inequality holding strictly for $0 < X(0) < K$.

Appendix S2: Empirical Methods

Data

We estimated several models of total annual fisheries catches per Large Marine Ecosystem (LME) across 53 LMEs during the period 1982-2006. We performed our analyses at the LME scale because catches in LMEs account for the bulk of global yields (Sherman & Duda 1999). The final dataset excluded several LMEs due to incomplete or unreliable catch or environmental data: Antarctica, Hudson Bay, Arctic Ocean, Arctic Archipelago, Baffin Bay/Davis Straight, Insular Pacific-Hawaiian, Gulf of Thailand, Indonesian Sea, East China Sea, Yellow Sea, East Siberian Sea, Laptev Sea, and the Kara Sea. The study window was determined by the availability of global catch and temperature data.

The model data relating to catch, temperature, and biodiversity come from three main sources (Table S1). Total annual catch histories, as well as the set of targeted species per LME, were obtained from the Sea Around Us Project (SAUP, available at http://seaaroundus.org). Temperature covariates were derived from the NOAA Optimum

Interpolation Sea Surface Temperature V2 dataset (provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, available at http://www.esrl.noaa.gov/psd/). The set of all fish species per LME and all fish trait data were extracted from FishBase (Froese & Pauly 2012).

Data for control variables

To account for the effects of several aspects of management on fisheries yields, for which time-series data could be compiled, we derived the following controls from several sources. First, to control for areas closed to fishing, we determined the presence/absence of Marine Protected Areas (MPAs) and the numbers of MPAs established between 1950-2006 using the MPA Global database (Wood 2007). Second, as an indicator of scientific robustness of management, we calculated the number of fisheries in an LME that had sufficient data for a (retroactive) stock assessment in a given year between 1950-2006. Data on stock assessment coverage were derived from the RAM Legacy Stock Assessment Database (Ricard *et al.* 2012). Third, we determined the presence/absence and number of individual quota (IQ) programs per LME and year, because IQ programs enforce a total allowable catch, and therefore directly alter total catch levels. Information on IQs, were derived from the Catch Shares Database from the Environmental Defense Fund (Environmental Defense Fund 2012). We present information about the derivation of each of these variables, including criteria for inclusion, at the end of the supplemental materials.

Derivations of covariates of interest.

Within-year temperature variability

Our primary measure of temperature variability, the coefficient of variation of sea surface temperature (SST CV), was computed in a two-step process using *NOAA_OI_SST_V2* available at *http://www.esrl.noaa.gov/psd/*. This raw SST data from NOAA contains monthly observations for each 1-degree grid cell from 1982-2006. The mean 'SST CV' variable is computed by first taking the within-year CV of monthly temperatures for a given cell, then averaging those CVs across all cells within an LME.

SST standard deviation

To assess the robustness of our results, we ran models with just the standard deviation (SST SD) of temperature. We computed the SD from the NOAA SST data; we first computed the within-year SD of temperatures for a given cell, then averaged those SDs across all cells within an LME.

Mean minus minimum SST: an indicator for upwelling potential and productivity

Martinez *et al.* (2009), Behrenfeld *et al.* (2006), and others have shown that in general, SST and productivity are inversely related. Wind-driven upwelling brings deep, cold water and nutrients (carbon, nitrogen, phosphorus, etc.) to replace warm, nutrient-depleted surface waters, which boosts biological production through the food chain from phytoplankton to fish to apex predators (Ware & Thomson 2005; Worm *et al.* 2005). Therefore, a pulse of cool water is a proxy for upwelling, and in effect, productivity. As a measure for within-year upwelling potential in an LME, we computed the per-cell difference between the lowest monthly SST and the average monthly SST in a given cell in a given year. Those values were then spatially averaged across all cells in an LME to produce a single measure of the difference between annual mean and minimum SST in an LME.

Diversity metrics and functional trait selection

Using both functional diversity (FD) and species richness (SR) allows us to examine if diversity in characteristics related to how species respond to or experience temperature fluctuations can offsets impacts of variation on catches. As SR calculations are straightforward, we cover only computation of FD metrics. These FD metrics have not yet been applied to global fisheries studies; the required data have only recently become available through the development of global fish trait databases like FishBase (Froese & Pauly 2012, available at www.fishbase.org/).

The first step in functional diversity calculation involved collecting trait information for all species from FishBase (Froese & Pauly 2012) using the 'FishbaseR' package version 0.9.3 in R (Cornejo-Donoso 2012). Trait values not available for a particular species were imputed based on values for similar species (see section on "Handling Missing Trait data" below). Next, we identified two sets of traits to be used for hypothesis tests. First, habitat preference and maximum depth were chosen as temperature-related traits that we expect to play a role in the mediation of temperature shocks. FishBase contains temperature ranges (minimum and maximum temperature) – traits ideal for testing our predictions – for a limited set of species; therefore, the fraction of species for which we had original, non-imputed temperature range values is small: <5% at species level and <25% at genus level (Fig. S1). Thus, we used habitat association and maximum depth range as proxies for temperature ranges and tolerances.

The categorical variable, habitat association, included categories of Bathydemersal, Bathypelagic, Benthopelagic, Demersal, Pelagic-Neritic, Pelagic-Oceanic, and Reef-Associated. We found that these traits were good proxies for temperature preference: of numeric traits with greater than 5% coverage, depth range maximum had the highest correlation with temperature traits, and all habitat types were significant predictors of temperature traits. This finding is consistent with a recent study (Rutterford *et al.* 2015). Matching with our theory, the maximum depth trait is a good proxy for T_{min}, and habitat association is likely closely associated with T^* (consistent with Clusella-Trullas *et al.* 2011).

Second, we selected traits we expect *not* to be directly related to how species respond to temperature variability -- trophic level and diet trophic level were selected. We refer to them as "trophic traits." Estimating models with diversity metrics based on trophic traits serves as a falsification test. A significant relationship between yield and diversity metrics based on trophic traits could be evidence of model misspecification, though we found no such relationship (Table S2).

For each set of traits, we derived functional diversity scores for targeted species and all fish species in each ecosystem. Specifically, we computed Functional Dispersion (Laliberté & Legendre 2010) of each species set for each group of traits, using the FD package in R (Laliberté *et al.* 2014). This metric was chosen because it is less sensitive to outlier species than alternatives, permits simple interpretations, and can be computed efficiently for large datasets (Laliberté & Legendre 2010). Functional dispersion measures the mean distance between a hypothetical "average" or "centroid" species and each species in the community. We define inter-specific distance as the Gower dissimilarity between species to include categorical traits and incorporate multiple traits into a single distance measure (Gower 1971). In that framework, two species with the same categorical trait value are considered identical (distance = 0), while species with different categorical trait values are considered maximally different (distance = 1). Distances based on continuous-valued traits are also scaled between 0 and 1. The average species corresponds to the centroid in the multidimensional-trait space defined by the traits of interest. We also scaled the resulting FD values to between 0-100. Functional Dispersion is already a normalized metric, but since the actual FD scores for different ecosystems need not occupy the full 0-1 range, we scaled the resulting values to facilitate comparisons across FD metrics defined using different trait sets.

Handling missing trait information

Unfortunately, the trait information available in FishBase contains missing information: many species records lack values for one or more traits (Fig. S1). As explained below, we selected traits for our analysis with the best coverage from among the traits relevant to the hypotheses. Still, not all species possessed values for all of the chosen traits. While Gower dissimilarity can handle some missing values, if a pair of species has no trait for which both species have valid values, the pair cannot be compared. To address this issue, we imputed trait values where measured values were not available. We did so using a process that assigns the group mean (continuous traits) or group mode (categorical traits) from a set of similar species. We attempted this imputation first using species from the same genus and the same LME. If that entire group lacked data on a specified group, we iteratively attempted to fill the missing value with groups of decreasing specificity. After the (1) same genus/ same LME group, we fall back on (2) same family/ same LME, (3) same genus/ any LME, (4) same family/ any LME, (5) any species/ any LME.

This process for filling in missing data has both advantages and limitations. At the global scale, a more detailed literature search to fill in missing values would be prohibitively time-intensive, and trait values for some species simply may not be known. Filling in values introduces information that is not actually observed, which will impact functional diversity calculations. By assuming that species take on median or mode values for traits with missing data, our approach deflates the computed diversity of a given community. General dampening of diversity scores toward zero could inflate coefficient estimates: differences in diversity measures are decreased when the absolute scores are deflated, and so a given difference in outcomes would be associated with a smaller difference in diversity. However, possible correlation between the diversity of a community and the number of missing trait values could produce the opposite effect. If more diverse (e.g. tropical) communities are better studied and more valid trait values are available, then the described imputation process would selectively dampen the diversity of less diverse communities, inflating cross-community differences in diversity and potentially biasing coefficients of interest downward. We expect that coefficient inflation due to overall dampening of diversity scores to be a larger effect, and more systematic examination of approaches to dealing with missing trait data is a potentially fruitful area for future research.

Computation of FD: Customized R code

Because of the size of our dataset (>10,000 species), computation of the Gower dissimilarity between species used custom R code. Consistency of functional diversity metrics across LMEs requires a single dissimilarity matrix for all species across all LMEs. To speed up this task, we computed unscaled dissimilarities at the LME level, found the trait range (for continuous-valued traits only) across all LMEs, and rescaled the LME-level dissimilarity scores using those ranges. This avoids computing dissimilarity among all pairs of species, instead calculating it only for species that coexist in at least one LME. Code is available upon request.

Model selection & robustness checks

Because equation 1 (main text) allows for flexibility in the choice of polynomial per-LME time trends, we examined the robustness of our results to those choices. We estimated versions of equation 1 with quadratic, cubic, and quartic per-LME time trends and compared models using both the Akaike Information Criterion (AIC) and Bayesian Information Critierion (BIC), which both seek to balance explanatory power with parsimony. We emphasize results with the best (lowest) BIC, because it more heavily penalizes model complexity based on the sample size and is therefore less likely to overfit the data. The model specification of equation 3 (main text) with the lowest BIC is the model for which we present the results in Table 1 of the main text.

In addition to examining the robustness of our results with respect to time trends, we also investigated whether other specific modeling choices impacted our results. Our results were not sensitive to the inclusion of different time trends (Table S3.A.), upwelling proxies (Table S3.B.) or lagged SST CV (Table S3.C.). The consistency of the coefficient estimates of interest across models is notable. Further, the direction and significance of our coefficients of interest was the same using the standard deviation of within-year SST (SST SD) as our temperature variability metric (Table S3.D).

The importance of trait selection

We tested the robustness of our results to trait selection because measures of functional dispersion are defined in terms of specific species traits (explained in “Diversity metrics” section). We examine how the offsetting effect of FD depends on trait selection by comparing FD metrics computed with temperature traits and with traits that we would not expect *a priori* to relate directly to species’ responses or susceptibility to temperature variability *per se*. Specifically, we use traits describing a species’ trophic level and the trophic level of its diet. Estimating models with diversity metrics based on those trophic traits serves as a falsification test. As expected, the offsetting effect of the functional diversity of the catch was not significantly different from zero when FD was computed with trophic traits not related to temperature preference (Table S2).

Dataset information: data processing for control variables

Management variables

Individual Transferrable Quota Programs

All of the forms of catch shares in the Environmental Defense Fund (EDF) database (available at http://apps.edf.org/page.cfm?tagID=57622) likely affect landings in some way, but we focused on management schemes that include an overall quota, which directly affect the level of yields. This included Individual Transferable Quotas (ITQs), Individual Fishing Quota (IFQs), Individual Vessel Quota (IVQs), and Individual Quota (IQs) programs.

Marine Protected Areas (MPAs)

MPA data came from the Wood (2007) database (available at www.mpaglobal.org). Only MPAs designated as having a subtidal component were included in the time series. This includes MPAs with both subtidal and intertidal components, but excludes those with intertidal components only. For MPAs with no data available to indicate subtidal or intertidal components, MPAs with the following designations from Wood (2007) were included in the derived time series: Biological Reserve, Conservation Park, Defined objective nature reserve, Ecological Reserve, Environmental Protection Area, Fish Habitat Area, Game Reserve, Integral Nature Reserve, Marine Management Area, Marine Park, Marine Protected Area, Nature Reserve, Other Area, Protected by Conservation Order, Protected Natural Landscape, Sanctuary, Special Area of Conservation, State Biological Reserve, Strict Nature Reserve, Wildlife Management Area, Wildlife Refuge, Wildlife Reserve and Wildlife Sanctuary. A number of MPAs in the database lacked information on the date of implementation. To obtain missing date information, an Internet search was conducted using the Google Search Engine for each MPA with absent data. Searches were standardized with a strict 5-minute search period using the search terms "*MPA [title],* established," "*MPA [title]*, designated" and "*MPA [title]*, established/designated, name of country or region."

Proxy for scientific robustness: No. of stock assessments per year

To determine the number of assessments by year and LME, we first matched the fished stocks from the RAM Legacy stock assessment database (2012 version) to LMEs (Ricard *et al.* 2012, available at http://ramlegacy.org/). Then, for all of the LMEs, we constructed a time series of the number of stock assessments that were conducted for stocks in a given LME. This covariate serves as a proxy for scientific robustness.

Supplemental Tables

Table S1. Explanation of covariates and their data sources used in the empirical analyses.

Covariate	**Explanation**	**Reference for data or use of covariate**
Species Richness of Catch (*SR catch* $_i$)	The number of different species caught by fisheries in each LME	Sea Around Us Project (2011) (available at www.seaaroundus.org/), also used in Worm *et al.* 2006; Chassot *et al.* 2010.
Species Richness of Ecosystem (*SR all fish* $_i$)	The number of different fish species in each LME	Fishbase (Froese & Pauly 2012) also used in Worm *et al.* 2006; Chassot *et al.* 2010.
Functional Diversity of catch (*FD catch* $_i$)	Functional dispersion was calculated using trait data on for only species targeted by fisheries in LME	Species in catch from Sea Around Us Project (2011) (available at www.seaaroundus.org/) with trait information from Fishbase (Froese & Pauly 2012).
Functional Diversity of ecosystem (*FD all fish* $_i$)	Functional dispersion was calculated using trait data on total fish community per LME	Fishbase (Froese & Pauly 2012).
Linear time trend ($P_i(t)$)	See *methods – flexible time trend to account for unobservable changes within a LME over time, such as a warming trend*	N/A
Cubic or quartic time trend ($P_i(t)$)	See *methods -- flexible polynomial time trend to account for unobservable, smooth changes within a LME over time*	N/A
Presence of	Controlled for closing	MPA Global database (Wood

Marine Protected Areas (MPA (yes/no) $_{it}$)	areas to fishing and a proxy for conservation interest by determining the presence/absence of MPAs in each LME between 1950-2006	2007).
Number of Marine Protected Areas (No. MPA$_{it}$)	Controlled for closing areas to fishing and a proxy for conservation interest by determining the number of MPAs in each LME and year (1950-2006).	MPA Global database (Wood 2007).
Mean minus minimum SST (Upwelling potential $_{it}$)	Mean minus minimum SST in the LME indicates upwelling potential	Data from NOAA (2014).
Number of individual quota programs (*No. IQs* $_{it}$)	Number of individual quota (IQ) programs per LME over time	EDF (2012) catch shares database; IQs enforce a total allowable catch.
Presence/absence of individual quota programs (*IQs (yes/no)* $_{it}$)	Presence/absence of individual quota programs per LME over time	EDF (2012) catch shares database.
Mean SST CV (SST CV$_{it}$)	CV of monthly SST in a given year and 1-degree cell, spatially averaged across all cells in an LME.	Data from NOAA OI SST V2 (NOAA/OAR/ESRL PSD).
Number of stock assessments (No. stock assessments $_{it}$)	Proxy for scientific robustness; a time series of number of stock assessments per LME and year	The RAM Legacy stock assessment database (Ricard *et al.* 2012).

Table S2. Linear regression results for log of total annual fisheries yields (in tonnes) by LME from 1982-2006 from a model with measures of functional diversity (FD) measured with the temperature-related traits and traits describing a species' trophic level and the trophic level of its diet. This model provides a comparison of FD measured with temperature-relevant traits versus other types of traits that we would not expect to have a mediating effect of temperature CV on yields in the current year (trophic level and trophic level of diet). The model uses clustered robust standard errors, per-LME intercepts, and per-LME polynomial time trends. For space, we exclude estimates of the per-LME intercepts and the per-LME time trends. The coefficients of interest, for which we test our main hypotheses, are significant ($p < 0.05$) and highlighted in bold.

	Estimate	**Std. error**	**t-value**	**p-value**
Upwelling potential	-0.001	0.05	-0.02	0.98
SST CV	**-103.79**	**57.05**	**-1.82**	**0.07**
MPAs* (yes/no)	-0.27	0.31	-0.88	0.38
(log) No. MPAs	0.03	0.08	0.42	0.67
(log) No. Stock assessments	-0.15	0.13	-1.19	0.24
IQs† (yes/no)	0.22	0.08	2.58	0.01
No. IQs	-0.05	0.04	-1.25	0.21
SST CV : (log) Temperature FD‡ catch	**20.71**	**5.52**	**3.75**	**<0.001**
SST CV : (log) Species richness catch	-18.72	24.84	0.75	0.45
SST CV : (log) Trophic FD§ catch	**5.41**	**10.71**	**0.51**	**0.61**
SST CV : (log) Temperature FD all fish	**-27**	**15.83**	**-1.71**	**0.09**
SST CV : (log) Species richness all fish	3.24	10.01	0.32	0.75
SST CV : (log) Trophic FD all fish	**2.05**	**7.83**	**0.26**	**0.79**

BIC: 264.6368 AIC: -908.1151

Adjusted R^2: 0.9933

** MPAs = Marine Protected Areas*

†IQs = Individual quota programs

‡ Temperature FD = Functional Dispersion measured with temperature-related traits

§ Trophic FD = functional diversity measured with trophic level and the trophic level of diet

Table S3. Tables A-D show the robustness of our results to other model specifications of equation 3. They include results from a linear regression model for log of total annual fisheries yields (in tonnes) by LME from 1982-2006. All models use clustered robust standard errors, per-LME intercepts, and per-LME polynomial time trends. For space, we exclude estimates of the per-LME intercepts and the per-LME time trends. The coefficients of interest, for which we test our main hypotheses, are significant ($p < 0.05$) and highlighted in bold.

A) Robustness of main results (Table 1) to inclusion of different time trends (here quartic trends versus cubic trends for which results are presented in the main paper).

	Quartic time trend		
	Estimate	Std. Error	p-value
SST CV	**-102.96**	**46.78**	**0.03***
Upwelling Potential	0.05	0.05	0.35
SST CV : (log) Temperature FD* catch	**18.38**	**5.77**	**<0.001****
SST CV : (log) Species richness catch	31.8	16.57	0.06 **.**
SST CV : (log) Temperature FD all fish	-33.61	12.62	0.01**
SST CV : (log) Species richness all fish	1.22	7.44	0.87
MPAs† (yes/no)	-0.28	0.24	0.25
(log) No. MPAs	0.1	0.08	0.22
(log) No. Stock assessments	-0.11	0.16	0.49
IQs‡ (yes/no)	0.15	0.06	0.02*
(log) No. IQs	-0.03	0.04	0.35
** FD = Functional diversity*	AIC: -1091.354		
† MPAs = Marine Protected Areas	BIC: 346.0452		
‡ IQs = Individual quota programs	Adjusted R^2: 0.9944		

B) Robustness of main results (Table 1) to inclusion of our proxy for upwelling potential (mean minus minimum SST) with cubic and quartic time trends.

	Cubic time trend			**Quartic time trend**		
	Estimate	Std. Error	p-value	Estimate	Std. Error	p-value
SST CV	**-113.48**	**53.18**	**0.03***	**-98.35**	**50.07**	**0.05***
Upwelling Potential	-	-	-	-	-	-
SST CV : (log) Temperature FD* catch	**21.76**	**5.49**	**<0.001*****	**16.89**	**6.07**	**0.01****
SST CV : (log) Species richness catch	24.25	20.45	0.24	29.89	19.57	0.13
SST CV : (log) Temperature FD all fish	-26.38	16.31	0.11	-32.25	13.66	0.02*
SST CV : (log) Species richness all fish	4.44	8.79	0.61	4.43	8.11	0.58
MPAs[†] (yes/no)	-0.27	0.3	0.38	-0.29	0.25	0.24
(log) No. MPAs	0.03	0.08	0.68	0.1	0.08	0.2
(log) No. Stock assessments	-0.15	0.12	0.23	-0.1	0.15	0.5
IQs[‡] (yes/no)	0.22	0.08	0.01**	0.15	0.06	0.02*
(log) No. IQs	-0.05	0.04	0.21	-0.04	0.04	0.33

** FD = Functional diversity*	AIC: -913.5588	AIC: -1089.593
† MPAs = Marine Protected Areas	BIC: 243.6256	BIC: 342.6176
‡ IQs = Individual quota programs	Adjusted R^2: 0.9934	Adjusted R^2: 0.9944

C) Robustness of results to inclusion of lagged effects of the coefficient of variation (CV) of sea surface temperature (SST CV_{t-1}) with cubic and quartic specifications of the main model (equation 3).

	Cubic time trend			**Quartic time trend**		
	Estimate	Std. Error	p-value	Estimate	Std. Error	p-value
SST CV_t	**-147.71**	**58.81**	**0.01***	**-146.49**	**50.51**	**<0.001*****
SST CV_{t-1} (lagged effect)	6.47	10.79	0.55	-0.66	10.61	0.95
Upwelling Potential	0.01	0.05	0.86	0.03	0.05	0.52
SST CV : (log) Temperature FD* catch	**20.81**	**4.92**	**<0.001*****	**19.52**	**5.07**	**<0.001*****
SST CV : (log) Species richness catch	29.88	19.94	0.13	36.92	16.39	0.02*
SST CV : (log) Temperature FD all fish	-20.66	13.53	0.13	-32.29	12.34	0.01**
SST CV : (log) Species richness all fish	2.18	9.3	0.81	3.9	7.53	0.6
MPAs† (yes/no)	-0.25	0.36	0.48	-0.4	0.28	0.16
(log) No. MPAs	0.07	0.08	0.4	0.13	0.1	0.18
(log) No. Stock assessments	-0.15	0.11	0.18	-0.09	0.16	0.56
IQs‡ (yes/no)	0.21	0.07	0.01**	0.15	0.07	0.04*
(log) No. IQs	-0.04	0.04	0.25	-0.03	0.03	0.4
** FD = Functional diversity*	AIC: -936.777			AIC: -1091.887		
† MPAs = Marine Protected Areas	BIC: 221.6008			BIC: 339.3526		
‡ IQs = Individual quota programs	Adjusted R^2: 0.9937			Adjusted R^2: 0.9946		

D) Robustness of results to a different measure of within-year temperature variability: the standard deviation (SD) of sea surface temperature (SST). The direction and significance of the main coefficients of interest are consistent with the main model (in Table 1).

	Estimate	**Std. error**	**t-value**	**p-value**
Upwelling potential	0.0002	0.06	-0.004	0.996
SST SD	**-0.38**	**0.19**	**-1.97**	**0.05**
MPAs (yes/no)	-0.27	0.30	-0.88	0.38
(log) No. MPAs*	0.03	0.08	0.41	0.68
(log) No. Stock assessments	-0.15	0.12	-1.21	0.23
IQs[†] (yes/no)	0.22	0.08	2.6	0.01
(log) No. IQs	-0.05	0.04	-1.25	0.21
SST SD : (log) Temperature FD[‡] catch	**0.07**	**0.02**	**4.06**	**<0.001**
SST SD : (log) Species richness catch	0.08	0.07	1.13	0.26
SST SD : (log) Temperature FD all fish	-0.09	0.06	-1.6	0.11
SST SD : (log) Species richness all fish	0.02	0.03	0.5	0.62

BIC: 475.839 AIC: -930.4254

Adjusted R^2: 0.9933

**MPAs = Marine Protected Areas*

† *IQs = Individual quota programs*

‡ *FD = Functional Diversity*

Table S4. Interpretation of marginal effects using coefficient estimates from the main model results (Table 1). Table S4 summarizes losses in yields (in tonnes) from historical variability with actual (current) level of FD of catch versus if the FD was reduced to the lowest observed FD.

Large Marine Ecosystem (LME)	**LME number**	**Tonnes of catch lost if FD reduced**	**S.E. of catch lost if FD reduced**	**Tonnes lost with offsetting effect of FD (actual level of FD)**	**S.E. of tonnes lost with actual level of FD**
Agulhas Current	30	-10207.4	4694.2	-1495.2	4325.2
Arabian Sea	32	-86765.9	39901.8	-38060.8	36812.2
Baltic Sea	23	-162285.8	74631.8	-30873.2	68645.1
Barents Sea	20	-89196.8	41019.7	-15150.0	37756.8
Bay of Bengal	34	-74347.9	34191.0	-13639.3	31455.4
Beaufort Sea	55	-32.5	14.9	-8.9	13.7
Benguela Current	29	-97874.4	45010.4	-13742.3	41484.3
Black Sea	62	-48563.2	22333.2	-8594.6	20551.1
California Current	3	-62078.1	28548.4	-9523.4	26295.7
Canary Current	27	-183064.9	84187.7	-26416.3	77577.8
Caribbean Sea	12	-15566.1	7158.5	-2898.6	6585.2
Celtic-Biscay Shelf	24	-124894.5	57436.3	-16921.1	52950.1
Chukchi Sea	54	-270.4	124.4	-71.8	114.2
East Bering Sea	1	-206782.3	95094.8	-41805.6	87435.3
East Brazil Shelf	16	-7083.7	3257.6	-1161.0	2999.2
East Central Australian Shelf	41	-1831.0	842.1	-286.1	775.5
Faroe Plateau	60	-14494.8	6665.9	-1662.8	6152.2
Greenland Sea	59	-21630.2	9947.3	-3108.5	9166.6

Guinea Current	28	-38783.2	17835.6	-5737.1	16432.4
Gulf of Alaska	2	-125946.7	57920.2	-24011.4	53273.4
Gulf of California	4	-26629.2	12246.2	-4844.6	11267.0
Gulf of Mexico	5	-67776.6	31169.0	-12258.6	28677.9
Humboldt Current	13	-757434.1	348327.9	-105798.1	321052.1
Iberian Coastal	25	-32446.7	14921.6	-4669.5	13750.3
Iceland Shelf/Sea	19	-78722.6	36202.8	-10466.5	33379.5
Kuroshio Current	49	-96653.7	44449.0	-13775.5	40962.7
Mediterranean Sea	26	-73439.7	33773.3	-10954.1	31114.5
New Zealand Shelf	46	-23925.2	11002.7	-3096.2	10146.5
Newfoundland-Labrador Shelf	9	-36722.0	16887.7	-5748.8	15552.9
North Australian Shelf	39	-4863.5	2236.6	-914.8	2057.4
North Brazil Shelf	17	-8794.6	4044.5	-1465.3	3723.2
North Sea	22	-363322.0	167084.1	-48300.4	154053.7
Northeast Australian Shelf	40	-3696.6	1700.0	-751.0	1563.0
Northeast U.S. Continental Shelf	7	-112423.5	51701.2	-20080.3	47572.8
Northwest Australian Shelf	45	-2973.5	1367.5	-500.7	1258.8
Norwegian Sea	21	-84954.6	39068.8	-11213.6	36023.7
Okhotsk Sea	52	-325658.0	149763.2	-46975.1	138005.0

Oyashio Current	51	-100639.9	46282.1	-15151.0	42635.8
Pacific Central-American Coastal	11	-38130.1	17535.2	-6299.9	16143.4
Patagonian Shelf	14	-111719.7	51377.5	-16520.1	47335.6
Red Sea	33	-6105.0	2807.6	-6105.0	2807.6
Scotian Shelf	8	-62957.3	28952.7	-11722.8	26633.8
Somali Coastal Current	31	-2586.2	1189.3	-478.7	1094.1
South Brazil Shelf	15	-11947.0	5494.2	-1747.5	5062.3
South China Sea	36	-260792.2	119932.8	-49516.4	110313.6
Southeast Australian Shelf	42	-1780.7	818.9	-271.3	754.3
Southeast U.S. Continental Shelf	6	-6068.4	2790.7	-1107.5	2567.5
Southwest Australian Shelf	43	-1427.1	656.3	-235.2	604.2
Sulu-Celebes Sea	37	-46770.7	21508.8	-10240.3	19768.1
West Bering Sea	53	-137379.1	63177.7	-25357.3	58120.7
West Central Australian Shelf	44	-1374.1	631.9	-213.2	582.0
West Greenland Shelf	18	-8687.0	3995.0	-1516.8	3676.5
Agulhas Current	30	-10207.4	4694.2	-1495.2	4325.2

SUPPLEMENTAL FIGURES

Figure S1. Global coverage of trait information at the species and genus levels varies greatly by trait (data from Fishbase, Froese & Pauly 2012). From left to right, traits are trophic level (TL), maximum age at maturity (ageMatMax), minimum age at maturity (ageMatMin), maximum depth (depthRangeMax), minimum depth (depthRangeMin), trophic level of diet (dietTL), habitat association (habitatAssoc), pelagic larval duration (larvalDuration), maximum observed length (length), length-weight parameters *a* and *b* from modeled relationships between length and weight (weight = $a*length^b$), main food, price category, reproductive mode, temperature range maximum, temperature range minimum, estimates of Von Bertalanffy model parameters (growth rate *k* and 'L infinity' *vbinf*, the asymptotic length). This information includes both continuous and categorical traits. The coverage for temperature range minimum and maximum was low (<5% at species level, <25% at genus level), but maximum depth range and habitat association had high coverage and are good proxies (see *diversity metric* section).

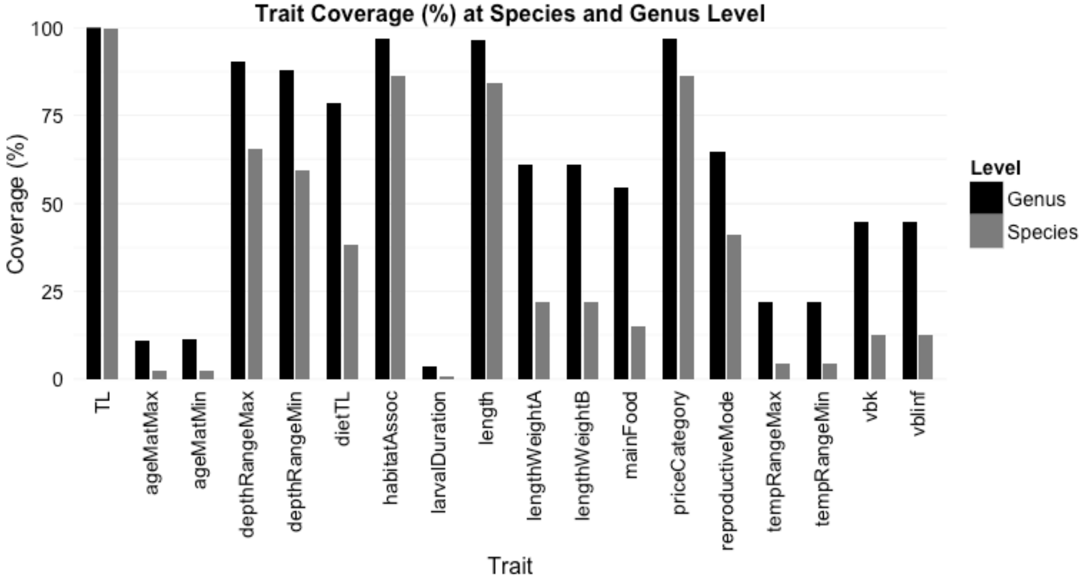
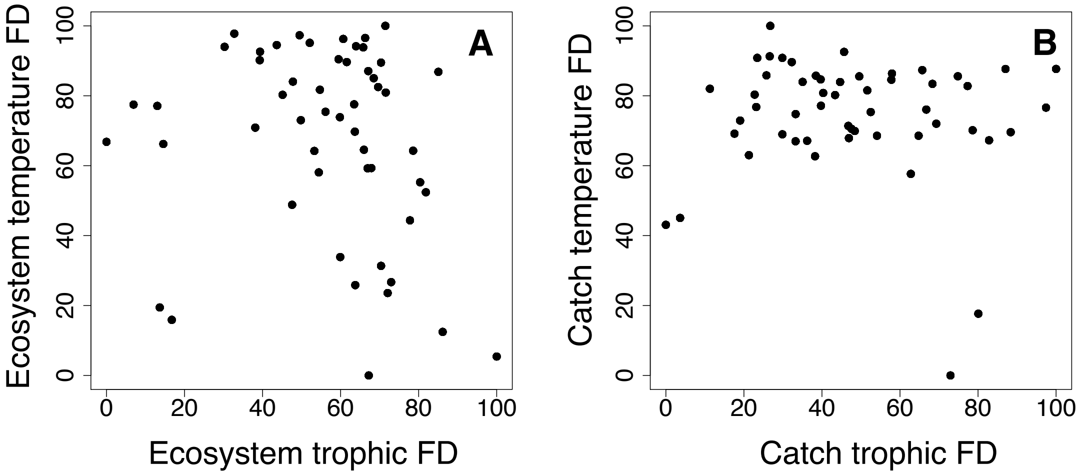


Figure S2. The information contained in functional diversity (FD) metrics depends on the trait sets used. This figure compares FD calculated with different sets of traits. “FD-temp” represents our “informed trait set” that characterize some aspects of how species may respond to changes in temperature, measured using habitat association and maximum depth as traits. In contrast, “FD-trophic” was calculated using trophic level and trophic level of diet as traits, which are not as directly related to species responses to temperature shocks *per se*. Observe that these FD metrics contain different information when describing both the ecosystem (all fish) and the catch diversity. FD metrics have been rescaled to fall between [0,100]. The two measurements of **A)** FD of the ecosystem (fish community) have very weak correlation (*r* = -0.174) and **B)** of FD of the catch are not correlated (*r* = -0.015).



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