The Economics of Biodiversity Loss*

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Abstract

We explore the economic effects of biodiversity loss by developing an ecologically-founded model of how different species interact to deliver the ecosystem services that contribute to economic production. Ecosystem services are produced by combining several complementary ecosystem functions such as pollination and water filtration, which are each provided by several substitutable species. Economic output is an increasing but concave function of species richness, and the marginal economic value of a species depends on: (i) how many redundant species remain within its ecosystem function, (ii) how critical the affected function is for overall ecosystem productivity, and (iii) the extent to which ecosystem services constrain economic output relative to other factors of production. We derive an expression for the fragility of ecosystems and economic output to further biodiversity loss. Ecosystem fragility increases with both mean species losses as well as the imbalance of species losses across ecosystem functions. Consistent with the model, we show that empirical measures of biodiversity degradation and ecosystem fragility are reflected in market assessments of risk in the cross-section of countries, which we extract from the prices of credit default swaps. We conclude by embedding our model of ecosystem service production in an intertemporal planning problem and study optimal land use when land use raises output at the cost of reducing biodiversity.

Keywords: Biodiversity Loss, Biodiversity-Productivity, Biodiversity-Stability, Nature-Related Risks, Biodiversity Stress Tests, Misallocation, Fragility

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In 2019, the *Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services* (IPBES) sounded the alarm. In its *Global Assessment*, the independent body tasked with providing policymakers with scientific assessments about the state of nature concluded that biodiversity was declining faster than at any time in human history. Reviewing a vast academic literature, the IPBES found that the global rate of species extinction was at least 10–100 times larger than the base rate over the past 10 million years, and is quickly accelerating, leaving about a quarter of animal and plant species groups threatened. The IPBES concluded that "*the great majority of indicators of ecosystems and biodiversity show rapid decline*" and that this decline of nature "*threatens a good quality of life.*"

In the years since this *Global Assessment*, biodiversity loss has increasingly attracted the attention of policymakers worried about its economic and financial implications. For example, in June 2023, Frank Elderson, Vice-Chair of the Supervisory Board of the European Central Bank (ECB), wrote that "*destroying nature means destroying the economy,*" announcing that the ECB would "*address the cascading effects of nature degradation and climate change on the economy and financial stability.*" In an interview with the Financial Times (2023) he expanded on this view, highlighting that "*biodiversity belongs in that list of things that affect the economy,*" and arguing that "*this is not some kind of a flower power, tree-hugging exercise...this is core economics.*" Similarly, World Bank researchers have concluded that an ecosystem collapse would cost about 2.3% of global GDP annually by 2030 (Johnson et al., 2021).

Given this increasing concern that biodiversity loss might significantly affect economic activity, there is a notable lack of research on the relationship between the two.[1] While a substantial literature has studied nature's contribution to economic growth, this is usually done by considering a monolithic stock of "natural capital" that enters the production function. While existing approaches have been helpful to understand some aspects of the economic importance of nature, they are silent on how to aggregate the totality of nature into this singular measure of natural capital. Indeed, by abstracting from the interactions between different species, these models have no role for bio*diversity*, and provide no framework for exploring how various species contribute to aggregate economic activity.[2]

In this paper, we aim to fill this gap by developing a model of how biodiversity affects aggregate economic activity. While the term biodiversity can encompass variation across a range of 'biotic scales'—from genetic variation within species to the global distribution of biomes—we follow the common use of the term to refer to the number of species present (Hooper et al., 2005). Concretely, our model describes how different species interact to produce the aggregate *ecosystem services* that enter more familiar economic production functions (see Daily, 1997; Daily et al., 2000; Chichilnisky and Heal, 1998; Heal, 2000; Dasgupta, Kinzig and Perrings, 2013). These ecosystem services include provisioning services such as food, fuel, timber, and raw materials for pharmaceutical R&D, as well as regulating services such as the provision of clean air and water, carbon sequestration, and pest and natural hazard regulation. Our production function for aggregate ecosystem services is grounded in insights from the ecology literature

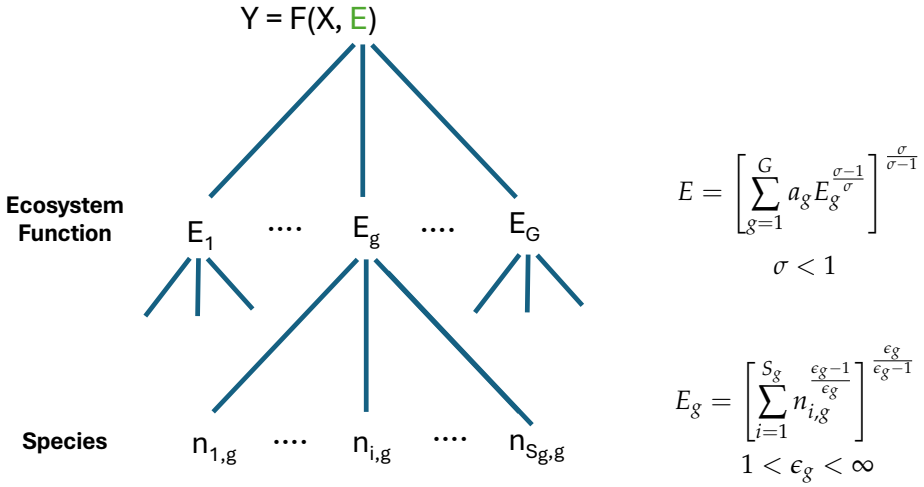
[1] This is in contrast to the more advanced work that integrates models of climate change and economic and financial activity (Nordhaus, 1991; Nordhaus and Boyer, 2003; Giglio, Kelly and Stroebel, 2021; Giglio et al., 2021; Barnett, Brock and Hansen, 2022; Barro, 2015; Weitzman, 2009). Similarly, work on the financial economics of biodiversity loss is only just emerging (Karolyi and Tobin-de la Puente, 2023; Giglio et al., 2023; Fenichel and Dean, 2024; Flammer, Giroux and Heal, 2025).

[2] In some cases, the literature has studied the interactions between different "natural capitals" in specific, small-scale, ecological settings (e.g., multi-species fisheries, as in Yun et al., 2017). However, as noted by Fenichel, Dean and Schmitz (2024), there have been few aggregated approaches to studying biodiversity-economy interactions.

but remains sufficiently tractable to be incorporated into more general economic models. It allows us to characterize the marginal economic values of different species and the fragility of ecosystem service provision, and thus helps to understand the sources of economic risks arising from biodiversity loss.

We model the production of aggregate ecosystem services in a hierarchical way, based on guidance from the ecology literature on how different species interact to contribute to a productive ecosystem (Diaz and Cabido, 2001; Hooper et al., 2005; Cardinale et al., 2012). Figure 1 presents a simple schematic of our model. Aggregate ecosystem services E enter the economic production function. The production function for ecosystem services has two layers. The top layer describes how different complementary ecosystem functions g contribute to the production of aggregate ecosystem services; the bottom layer describes how each ecosystem function, in turn, is produced by the interaction among substitutable species, with $n_{i,g}$ being the abundance of species i contributing to function g.

Figure 1: Ecosystem Service Production



Note: Figure sketches our hierarchical model for the production of ecosystem services, E, as a function of the abundances of different species $n_{i,g}$ across functional groups g. The model is formally described and specified in Section 1.2.

At the top level, we capture that the aggregate output from a healthy ecosystem depends on the often complex interactions of many different ecosystem functions, including those referred to as 'regulating' and 'supporting' functions: pollination, nutrient recycling, water purification, pest control, and many more. We model the combination of these functions into an aggregate ecosystem service flow via a constant-elasticity-of-substitution (CES) aggregator familiar to economists (see Arrow et al., 1961; Dixit and Stiglitz, 1977). Consistent with insights from the ecology literature, different functions are complements in the production of aggregate ecosystem services (i.e., they have an elasticity of substitution $\sigma < 1$), capturing the idea that healthy and productive ecosystems are hard to sustain when key functions are missing and that a decline in the availability of one function cannot easily be compensated for by the growth of other functions (Sekercioglu, 2010; Fenichel, Dean and Schmitz, 2024; Potts et al., 2016).

At the bottom level, we model how different species interact to produce each specific ecosystem function. Here, our model captures that there are usually multiple species playing similar functional roles (e.g., many insect species provide pollination services). We assign each species to its primary

ecosystem function, and model the total output of a function as another CES aggregator across the number of individuals in each species. Within this function-level aggregator, different species are highly substitutable, but not perfectly so (i.e., the elasticity of substitution is $1 < \epsilon < \infty$). This approach implies that a function with two species of 50 members each has higher output than a function with 100 members of a single species and is consistent with the "biodiversity-productivity" relationship documented in the ecology literature, which has found function-level output to be an increasing function of species richness (Hooper et al., 2005; Tilman, Isbell and Cowles, 2014). This relationship results from *niche differentiation*, whereby different species in the same function vary on dimensions that ensure they inhibit other species less than members of their own species. For example, when plant species with roots of different lengths are present, more nutrients can be extracted and a larger biomass sustained than in monocultures.

Our model captures an important feature of the within-function "biodiversity-productivity" relationship, its *concavity*: while increases in biodiversity tend to have positive effects on output, the marginal benefits decline as more and more species are present. This also means that the loss of a species will have less severe consequences in a species-rich ecosystem relative to a biodiversity-degraded one: the presence of many species that can all perform a similar function in a species-rich ecosystem ensures functional redundancy, and represents a form of diversification with respect to the risk of extinction of some of the species. This concavity also implies that species losses have increasingly larger and larger effects on both ecosystem service production and the fragility of the ecosystem to further species losses. In the extreme case, when biodiversity is sufficiently deteriorated, a few species may become "keystone species": species whose extinction will lead to large negative effects on ecosystem and economic output.

The concavity that arises from the interaction of species *within* each function, gets further amplified through the interaction *across* different complementary function in the top layer. Even when species loss in a function has become large enough to affect the function-level output, this will only start affecting the production of aggregate ecosystem services when the function has sufficiently deteriorated to become a constraining function for aggregate production.[3] Therefore, through the combination of the two hierarchical layers, each introducing a different source of concavity, our model can generate substantial (and realistic) non-linearities and tipping points that have been discussed in the ecology and biodiversity literature (e.g., Svartzman et al., 2021; Fenichel, Gopalakrishnan and Bayasgalan, 2015).

Having specified the hierarchical structure of our ecosystem production function, we characterize the aggregate impact of a biodiversity shock—a loss to a set of species across multiple functions. Specifically, we derive a decomposition reminiscent of the literature on the economic effects of input misallocation across firms (Hsieh and Klenow, 2009; Baqaee and Farhi, 2019*b*). The decomposition allows us to distinguish the direct effects of biodiversity loss on production (because some species have disappeared and therefore cannot participate in the production of ecosystem services) from the additional effects when losses are asymmetric across functions: because of the output of each function is concave in the number of species, losses that are concentrated in a few functions may be much more problematic than losses spread out more uniformly across many functions (taking the average loss as given).

[3]The intuition for this is clearest in the case of extreme complementarity, where the CES aggregator collapses to a Leontief function in which the overall level of ecosystem service provision is given by the productivity of the least productive function. In such a setting, biodiversity loss in a given function only reduces aggregate ecosystem output when that function has become the least productive, with zero effects from biodiversity loss in other functions.

In addition to the general decomposition of the response to an arbitrary biodiversity shock, we also derive a single, tractable measure of the *fragility* of ecosystem services, defined as the vulnerability of aggregate ecosystem services to a uniform shock across species. We show that our fragility measure combines information about the average state of biodiversity as well as the imbalances within and across functions, representing a measure of the vulnerability of ecosystem to future shocks. This measure therefore captures a notion of *biodiversity risk* that can be brought to the data.

The next step in integrating biodiversity into the economic system is incoporating the role of ecosystem services in the aggregate economic production function (the F at the very top of Figure 1). Following a large literature, we propose an economic production function that uses ecosystem services as complements to other factors of production (land and capital) to capture the idea that it is hard to substitute for the loss of ecosystem services through an increased use of other factors (Cohen, Hepburn and Teytelboym, 2019; Dasgupta, 2021). The relationship between economic output and biodiversity loss inherits many of the properties of the relationship between biodiversity loss and the production of aggregate ecosystem services. The complementarity between factors of production further amplifies the concavity of the relationship between biodiversity and output: losses of aggregate ecosystem services in response to biodiversity loss will only affect aggregate economic output if those ecosystem services—and not, for example, the availability of physical capital—are the primary constraint on aggregate output.

We then provide empirical evidence on the effects of biodiversity loss on economic activity. Given our emphasis on the aggregate effects of biodiversity loss, our empirical work focuses on a cross-country analysis.[4] Studying the macroeconomic effects of biodiversity loss is complicated by two factors. First, such effects will manifest over long horizons and at low frequencies. And second, as long as the current state of biodiversity is not too degraded, our model suggests that biodiversity loss should largely increase the risks from future biodiversity losses (though raising ecosystem fragility) without having large affect on current macroeconomic aggregates. For these reasons, we focus our analysis on country-level measures of (forward-looking) *risk* that allow us to capture countries' exposures to future biodiversity loss, are available at high frequency, and that map to the model through the concept of *fragility*. We do so by studying the prices of sovereign credit default swaps (CDS), which measure investors' perceived probability that a country will default on its debt.

In our weekly panel of 79 countries for 21 years, we show that CDS spreads tend to increase on average when investors receive negative news about aggregate biodiversity loss, as measured by Giglio et al. (2023). While this average effect is consistent with the fact that negative biodiversity news makes the global economy riskier, it is not statistically significant, in part because biodiversity risk might not be substantial in many countries and in part because many other macroeconomic events affect average global CDS spreads, making it difficult to tease out the aggregate movements due to biodiversity risk.

We then exploit the *cross-sectional* variation in biodiversity risk exposures across countries to provide evidence for several key predictions from our model. First, we show that negative biodiversity news induces significant increases in CDS spreads specifically for those countries with relatively more depleted ecosystems as captured by several distinct indicators of ecosystem health. Second, we find that

[4] Aggregate biodiversity loss will percolate through the various sectors and firms in the economy. At that level of disaggregation, both physical biodiversity risks and regulatory (transition) risks will become relevant. We do not study these firm- and industry-level effects in this paper, but refer the interested reader to Giglio et al. (2023).

CDS spreads increase more significantly upon negative biodiversity news in countries where ecosystem services are more likely to be the constraining factor for aggregate output. Third, we show that *imbalances* in past biodiversity loss across functions increase a country's biodiversity risk exposure. To test this prediction, we join data from the Map of Life project (Jetz, McPherson and Guralnick, 2012), that collects species-level data on relative changes in habitat sizes—and thus proxies for the loss of the species that rely on that habitat—with taxonomic classification from the TetrapodTraits data (Moura et al., 2024), which maps each species into proxies for their primary ecosystem functions. Therefore, we can construct an empirical counterpart for the imbalance in species loss across functions that our model predicts should determine ecosystem fragility. Our empirical analysis shows that, indeed, countries where the *dispersion* in losses across species were larger experience higher CDS spreads in response to negative biodiversity news compared to countries with lower imbalance.

In the final part of the paper, we consider the interactions between economic activity and biodiversity loss and their implications for the optimal use of natural resources. Since land-use changes are the key driver of global biodiversity loss (IPBES, 2019), we solve for the optimal land use trading off the immediate gains in economic output and against the long-term economic costs of biodiversity loss. Our intertemporal model highlights ecosystem fragility as a crucial driver of optimal land use, or equivalently land conservation. Land conservation policies should be particularly strong in countries have already suffered large and dispersed species losses, and in capital-rich economies where ecosystem services are more likely to be the constraining factor of production.

Implications. Our integrated model of nature, biodiversity, and the economy presents several implications for researchers and policy makers hoping to better understand the economic effects of biodiversity loss. Most directly, it highlights the weakness of one of the most common attempts to dismiss the potential importance of biodiversity loss for economic activity: that the large biodiversity losses in the past century have not seemingly led to significant declines in current economic output. As the model shows, the non-linear relationship between species richness and economic output implies that current losses might have limited economic impact even while they increase the risk of *future* losses, as biodiversity is depleted within functions and species and functions become critical (keystone). In fact, our empirical analysis shows that precisely those risks are already reflected in forward-looking asset markets.

Our modeling approach also emphasizes that different species are differentially important for overall ecosystem service production, and thus economic activity. The relative importance of each species is context dependent and varies with the presence of other species in the same ecosystem function as well as the marginal importance of the particular function within its ecosystem. Our modeling framework generates simple expressions for the relative marginal importance of each species, and can be then used for a variety of policy purposes. First, it can inform the optimal design of Pigouvian taxes on economic activities that might lead to local extinctions of various species. Second, it provides a tool to think about the prioritization of conservation efforts in a world where society's willingness pay for nature protection is finite. Third, it can be helpful to determine appropriate 'exchange rates' across activities affecting different species in the design of biodiversity offsets in which firms aim to compensate for specific negative biodiversity effects of their activities through conservation efforts that protect other dimensions of biodiversity (McKenney and Kiesecker, 2010).

1 The Production of Ecosystem Services

In the following sections, we develop a tractable model to explore the effects of biodiversity loss on aggregate economic activity. We begin by considering a homogeneous firm with production function:

$$Y = F(\mathbf{X}, E). \tag{1}$$

The variable E denotes *ecosystem services* that contribute to the aggregate economic production process. These include provisioning services (e.g., food, fuel, and raw materials) and regulating services such as the provision of clean air and water, carbon sequestration, and pest regulation (Millennium Ecosystem Assessment, 2005; OECD, 2023). The vector $\mathbf{X}$ denotes other factors of production such as physical capital and labor. For simplicity, we focus on a single final economic good Y that is produced using a single flow of aggregate ecosystem services E. In other words, while ecosystem services and production can vary by geography, we model the production without explicitly specifying location—with the idea that different locations will face different environments but similar structures for the production function.[5]

We next review insights from the ecology literature on important implication of biodiversity for ecological outcomes. A key contribution of our work is to then propose a tractable approach to modeling the aggregation of the individual contributions of various species to the production of E in an ecologically-founded way that allows the integration of these insights into existing economic frameworks.

1.1 Ecosystem Service Production: Insights from the Ecology Literature

Ecosystems are commonly defined as the collection of the living things in an area (e.g., plants, animals, and organisms) and their interactions with each other and non-living parts of nature such as water and soil. These interactions jointly produce the ecosystem services that enter economic production.

Motivated by the "*growing consensus [. . .] that functional diversity, or the value and range of species traits, rather than species numbers per se, strongly determines ecosystem functioning*" (Diaz and Cabido, 2001), ecologists studying the contributions of various species to ecosystem productivity often characterize species as members of "functional groups" that include different species fulfilling similar primary ecosystem functions. (Tilman, 2001; Hooper et al., 2005; Oliver et al., 2015). Based on this classification, researchers then frequently analyze the interaction between species within functional groups separately from the interaction of different functional groups to maintain overall ecosystem health.

Complementarity Across Ecosystem Functions. Healthy ecosystems are based on complex interactions between species in different functional groups. Following Hannon (1973), researchers often describe these interactions and interdependencies using "ecosystem networks" similar to input-output networks

[5]Our ecologically founded mechanism for the economic benefits of biodiversity is distinct from work by Polasky, Solow and Broadus (1993) and Polasky and Solow (1995), who focus on the option value of different species in providing possible future benefits, for example in the pharmaceutical R&D process. In our model, we focus on the immediate benefits of biodiversity in terms of facilitating more productive and less fragile ecosystems. In later sections, we allow species to provide another direct benefit to humans through the provision of "cultural ecosystem services", which capture, for example, recreational or other benefits that nature—and in particular "cute" or emotive species—provide to humans. Those benefits will be modeled by allowing utility to directly depend on E. Our approach thus sidesteps the broader ethical question of whether the value of nature is best approached from the anthropogenic perspective of the loss of ecosystem services that are useful to humans–whether directly or through increasing economic output—or whether species existence should be given weight per se.

in economics.[6] Important conclusions from this literature are that: (i) healthy ecosystems are hard to sustain when a key ecosystem function is missing (Szyrmer and Ulanowicz, 1987; Rapport, Costanza and McMichael, 1998; Williams et al., 2002; Felipe-Lucia, Comín and Bennett, 2014); (ii) there are positive interaction effects between different ecosystem functions, whereby "*the loss or decline in any single ecosystem service [. . .] is likely to reduce the productivity of other ecosystem services.*" (OECD, 2023; Fridley, 2002; Lundin et al., 2013; Garibaldi et al., 2018; Chen et al., 2022; Martínez-Salinas et al., 2022); and (iii) in any given ecosystem, growth in less abundant resources or functions has the largest effects on overall ecosytem productivity (Sperfeld, Martin-Creuzburg and Wacker, 2012; Garibaldi et al., 2018; Fijen et al., 2020). Below, we show that all of these insights can be captured through modeling a low elasticity of substitution between functional groups in the production of aggregate ecosystem services.

Species Substitutability within Ecosystem Functions. A first key finding regarding the effects of species richness within functional groups is that more diverse functions are more productive, with smaller productivity gains from increases in the number of species at higher levels of biodiversity. In other words, the productivity of an ecosystem function is an increasing and concave function of biodiversity. Discussing the evidence for this "biodiversity-productivity relationship," Tilman, Isbell and Cowles (2014) conclude that "*by 2006, the preponderance of evidence from more than 100 biodiversity experiments had shown that species diversity had a repeatable and consistent effect on productivity.*" For example, various experimental studies found that total plant productivity on a fixed plot of land was an increasing function of plant diversity, with smaller marginal effects at higher levels of diversity (Naeem et al., 1995; Tilman, Wedin and Knops, 1996; Hector et al., 1999). Similarly, based on a large-scale observational study, Liang et al. (2016) conclude that "*using ground-sourced data from 777,126 permanent plots, spanning 44 countries and most terrestrial biomes, we reveal a globally consistent positive concave-down biodiversity-productivity relationship.*"

A prominent theory for the positive relationship between species richness and function-level productivity is "niche differentiation." Hooper et al. (2005) explain the underlying mechanism as follows: "*If species use different resources, or the same resources but at different times or different points in space, more of the total available resources are expected to be used by the community. If those resources limit growth, then increasing functional richness should lead to greater total productivity.*" In other words, "*each species inhibits itself more than it inhibits the other species*," allowing for a larger community abundance—that is, more individuals or more biomass—in more diverse functions (Tilman, Isbell and Cowles, 2014).[7] For ex-

[6] Some groups of species have mutualistic relationships, whereby members of each functional group benefit from the presence of the others. For example, plants and pollinators each rely in each other for their existence: the pollinator benefits by feeding on the nectar and pollen provided by the flower, while the plant benefits from the ability to reproduce as the pollinator transfers pollen as it moves between flowers. Other bilateral relationships between functions are more antagonistic, for example those between predator and prey or those between herbivores and plants.

[7] A second mechanism that can contribute to higher productivity in more diverse functions is "selection" or "sampling", whereby overall functional productivity is disproportionately determined by the presence of highly productive species, and increasing species richness raises the chance that those highly productive species are present (Tilman, Lehman and Thomson, 1997; Loreau, 2000). However, while selection mechanisms can contribute to the observed biodiversity-productivity relationship, the frequent observation of transgressive overyielding—when the productivity of a species mixture is higher than the productivity of the most productive species in a monoculture—affirms an important role for niche differentiation. In addition, Hooper et al. (2005) concluded that "*ecologists disagree over whether sampling effects are relevant to natural ecosystems*" or only an artifact in some experimental set-ups. To the extent that both forces are at work, "*complementarity effects typically increase over time, leading to increased overyielding as plant communities mature, while selection effects decrease*" (He et al., 2024). As a result, we focus our model on capturing effects of biodiversity on productivity through niche differentiation.

ample, when ecosystems contain plants with different root lengths, more of the available nutrients can be extracted than when there are fewer species with roots of similar lengths competing for the same resources (Loreau, 1998). Similarly, more diverse forests with tree crowns at varying heights can use the available light more effectively, leading to increased total stem biomass (Williams et al., 2017). And when different pollinator species are active at different times of the day, overall crop yield can rise with species diversity even holding fixed the total number of individual pollinators (Hoehn et al., 2008).

A second key finding in the ecology literature is that the output of ecosystem functions varies less over time in response to environmental fluctuations and species loss when the baseline level of biodiversity is higher. The ecological mechanism for such a "biodiversity-stability relationship" is functional redundancy—having multiple species within a group performing a similar function—combined with compensatory growth, the "*widely observed process in which one species within a functional group increases in response to the reduction or loss of another in the same functional group*" (Naeem and Li, 1997). Hooper et al. (2005) describe the mechanism as follows: "*If an ecosystem is subject to a variety of natural and human caused environmental stresses or disturbances, then having a diversity of species [...] ought to reduce the likelihood of loss of all species capable of performing particular ecological processes. [...] As some species do worse, others do better because of different environmental tolerances or competitive release. [...] In this sense, redundancy of functional effect traits [...] act as insurance in carrying out ecological processes.*" Evidence for this positive biodiversity-stability relationship has been found in many experimental and observational studies (e.g., Naeem and Li, 1997; McGrady-Steed, Harris and Morin, 1997; Gross et al., 2014; Bai et al., 2004).

Below, we show that both the biodiversity-productivity relationship and the biodiversity-stability relationship can be captured by a high but finite elasticity of substitution between species within an ecosystem function in the production of the ecosystem services produced by that function.[8]

1.2 Modeling Approach

Based on these insights, we model the production of aggregate ecosystem services E in a hierarchical way, which we sketch in Figure 1. We assume that each species belongs to an ecosystem function indexed by $g = 1, \ldots, G$, where the number of functions G is fixed.[9] These functions include groups of species providing the same primary ecosystem services E_g, such as soil fertilization, pollination, water purifi-

[8]The insight that more diverse systems are more resilient and productive might, at first sight, appear to conflict with the observation that modern agriculture often uses monocultures, the planting of vast areas with a single crop. However, monoculture agriculture is driven by technological reasons rather than biological ones, and practical considerations related to the ease of planting, managing, and harvesting monocultures have led to their proliferation *despite* the negative effects on long-run productivity, which include degraded soil health and increased vulnerability to pests and diseases (CSANR, 2023; Decker et al., 2022). Increasingly popular practices like intercropping—the practice of growing two or more spatially intermingled crops—allow farmers to benefit from the positive biodiversity-productivity relationship to increase overall yields and profitability, in particular in countries with labor-intensive agricultural production (Li et al., 2021). Similarly, the practice of crop rotation, which varies the monoculture grown between years, attempt to mitigate some of the biological weaknesses of monoculture agriculture while maintaining the productivity advantages of mechanized harvesting (Wang et al., 2023).

[9]Since we will allow for arbitrary correlations between species loss shocks across functions, nothing prevents a species from belonging to multiple ecosystem functions. Concretely, imagine a species contributing to two functions. We would model this species separately as a member of each function, but assuming a correlation between extinction shocks to the two functions. The practical challenge of delineating functional groups is well appreciated in the ecology literature, and different definitions of functional groups can be helpful for different purpose (Petchey, O'Gorman and Flynn, 2009). While cutting the "function space" too narrow will lead to a mechanical convergence of functional and species diversity, the other extreme of grouping different functional groups together may miss large declines in ecosystem productivity from the loss of species with little actual functional redundancy (see the discussions in Naeem and Wright, 2003; Cadotte, Carscadden and Mirotchnick, 2011).

cation, the production of energy for others through photosynthesis, or carbon sequestration—functions that, as described above, are complementary in the production of aggregate ecosystem services. Within each function, there are S_g unique species, indexed by $i = 1, \ldots, S_g$, with a population $n_{i,g}$ of each species. We start with the description of ecosystem service production within each function, E_g, before turning to the aggregation of the various functional groups to produce aggregate ecosystem services, E.

1.2.1 Substitutability of Species Within Each Function

The species in each function produce a flow of ecosystem services E_g through a constant elasticity of substitution (CES) aggregator across the different species' populations, with elasticity of substitution ϵ_g:

$$E_g = \left[\sum_{i=1}^{S_g} n_{i,g}^{\frac{\epsilon_g - 1}{\epsilon_g}} \right]^{\frac{\epsilon_g}{\epsilon_g - 1}}. \tag{2}$$

Consistent with the evidence from the biodiversity-productivity relationship reviewed above, we assume that, within each function, species are highly, but not perfectly, substitutable:

$$1 < \epsilon_g < \infty.$$

If species become perfect substitutes, $\epsilon_g \to \infty$, then equation (2) is just given by the sum of populations across species $E_g = \sum_{i=1}^{S_g} n_{i,g}$. A finite elasticity captures that, due to niche differentiation, species are not perfect substitutes in terms of ecosystem services production.

Denote as $\bar{S}_g > 1$ the initial, maximal, number of species in functional group g, and let $s_g = S_g / \bar{S}_g$. We focus on biodiversity loss, that is what happens when $S_g \leq \bar{S}_g$. When S_g falls, surviving species in group g grow in response to the decreased competition for common resources, consistent with the ecological evidence for compensatory growth. In principle this could be modeled using Lotka-Volterra models, which describe a full dynamic system governing the evolution of abundances in response to species loss (see Hofbauer and Sigmund, 1998). Instead of solving for the dynamic path of such models, we focus on the rest point of the system and assume adaptation depends on a simple parameter $\alpha_g \in [0, 1]$. For simplicity, we also impose symmetry among the remaining species in a function, so that $n_{i,g} = n_g$ for each $i = 1, \ldots, S_g$.[10] With these assumptions, each species' abundance is given by:

$$n_g = \bar{n}_g \left(\frac{\bar{S}_g}{S_g} \right)^{1-\alpha_g} = \bar{n}_g s_g^{\alpha_g - 1}. \tag{3}$$

Equation (3) implies that function g's *community abundance* (i.e., total population or biomass),

$$N_g = S_g n_g = (\bar{S}_g \bar{n}_g) s_g^{\alpha_g},$$

is equal to a share $s_g^{\alpha_g} \in [0, 1]$ of its maximal level, $\bar{S}_g \bar{n}_g$. The parameter $\alpha_g \in [0, 1]$ captures the extent of compensatory growth of remaining species, and can depend on both the time horizon and the degree of crowding out due to competition for common resources between species in the same function.

[10] In Appendix C.1, we show how to expand this exposition to incorporate within-function variation in populations via Hill (1973) numbers that measure the "effective number of species" (see also the discussion in Fenichel, Dean and Schmitz, 2024).

The polar case $\alpha_g = 1$ implies that $n_g = \bar{n}_g$ and thus captures the short run: following the loss of a species, the remaining species are still at their previous level. Alternatively, $\alpha_g = 1$ can capture long-run equilibria of community abundance in a function where different species do not compete for similar resources, and so the population of one species does not vary with the presence of other species; in this case, the loss of one species does not induce compensatory growth of the remaining species.

The other polar case, $\alpha_g = 0$, implies that $S_g n_g = \bar{S}_g \bar{n}_g$ and the surviving species expand to fully offset any species loss in terms of community abundance within a function. This substantial compensatory growth corresponds to an environment where competition for common resources is so intense that each member of a species in a function one-for-one crowds out another species member in that function.

In practice, values of α_g between 0 and 1 are most consistent with the empirical evidence. Plugging n_g into the within-function aggregator given by equation (2), ecosystem services from function g equal:

$$E_g = \underbrace{(\bar{S}_g \bar{n}_g) s_g^{\alpha_g}}_{\text{Community Abundance } N_g} \times \underbrace{(\bar{S}_g s_g)^{\frac{1}{\epsilon_g - 1}}}_{\text{Gains from Biodiversity}} . \tag{4}$$

The variables α_g and ϵ_g thus allow for a separate parametrization of the two forces through which biodiversity can increase E_g: (i) the ability to sustain a more abundant community due to spatial or temporal variation in resource use, with the effects increasing when there is less competition for common resources (high α); and (ii) an increase in productivity for a fixed community abundance due to temporal and other variation in performing the ecosystem service, with larger effects when species are more differentiated (low ϵ_g). Ultimately, function g's ecosystem service production E_g becomes:

$$E_g = \bar{E}_g s_g^{\phi_g}, \tag{5}$$

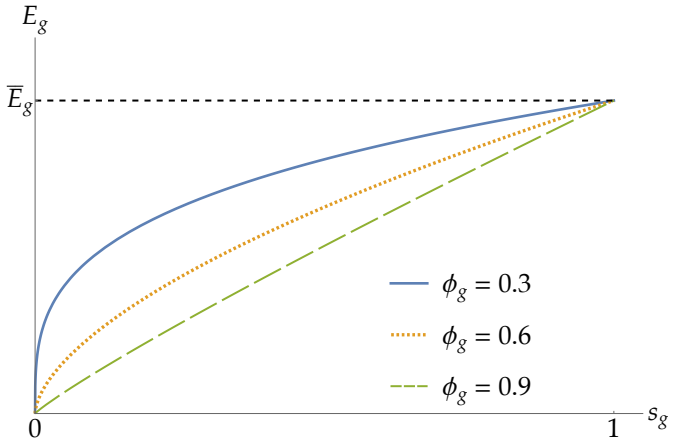
where the exponent ϕ_g captures how substitutable species are and how much crowding out there is:

$$\phi_g = \frac{1}{\epsilon_g - 1} + \alpha_g, \tag{6}$$

and $\bar{E}_g = \bar{n}_g \bar{S}_g^{\epsilon_g/\epsilon_g - 1}$ is the maximum level of ecosystem services attained absent species loss ($s_g = 1$). We impose $\phi_g < 1$, consistent with the empirical observation of a "*positive concave-down biodiversity-productivity relationship*" in the ecology literature (Liang et al., 2016). The concavity of E_g with respect to s_g is also consistent with the previously discussed evidence for a positive biodiversity-stability relationship within a function. Specifically, while often treated as separate observations, the concave biodiversity-productivity relationship immediately delivers the biodiversity-stability relationship: when a function is at the species-rich flat part where additional diversity has only small positive effects on productivity, the loss of a particular species has equivalently small negative effects on productivity.

Figure 2 shows how E_g varies with s_g for different values of ϕ_g. A value $\phi_g = 0.3$ is consistent with estimates from Liang et al. (2016) and the meta-analysis in O'Connor et al. (2017) and can be viewed as capturing the long-run effect of species loss after compensatory growth has allowed the abundance of remaining species to rise. Higher values of ϕ_g imply lower ecosystem services production E_g, and can capture the impact of species loss at shorter horizons before surviving species had time to grow.

Figure 2: Ecosystem Service Production and Biodiversity, Within Group



Note: Figure shows output of function g, E_g, as the remaining number of species, s_g varies, for different values of ϕ_g.

1.2.2 Complementarity Across Functions

Overall ecosystem services are modeled as aggregating the different ecosystem functions E_g through another CES aggregator, where each function is weighted equally to simplify notation:[11]

$$E = \left[\sum_{g=1}^{G} E_g^{\frac{\sigma-1}{\sigma}} \right]^{\frac{\sigma}{\sigma-1}} \quad \text{where} \quad \sigma < 1. \tag{7}$$

While substitutability across species is high *within* functions, higher-level ecosystem functions are complements in the production of aggregate ecosystem services: the elasticity of substitution across functions satisfies $\sigma < 1$.[12] Consistent with the empirical ecology literature, this restriction on σ ensures that E goes to zero when any one function is missing entirely.

It is possible to further calibrate σ by comparing the effect of individual and joint increases in the availability of different ecosystem functions on overall ecosystem output. Through the lens of equation (7), the lower the sum of individual marginal effects relative to the joint effect, the lower the elasticity of substitution σ must be. For example, Sutter and Albrecht (2016) studied the joint influence of pest control and pollination on ecosystem functioning, finding "*strong synergistic effects of insect pollination and simulated pest control on yield quantity and quality. Their joint effect increased yield by 23% [...], while their single contributions were 7% and 6%, respectively.*" These estimates imply a very low elasticity of substitution between pollination and pest control: calibrating our CES specification to match these reported effects suggests $\sigma \approx 0.1$ (see Appendix B.1 for details on this calculation).

[11] While it would, in principle, be possible to formally model an input-output network linking the various ecosystem functions, the CES aggregator allows us to capture the key insight from those networks—namely that ecosystem functions are complements, and that well-functioning ecosystems depends on the health of each function—in a tractable way.

[12] An extreme version of this idea is attributed to von Liebig (1855). His "law of the minimum" is described by Gleeson and Tilman (1992) as follows: "*Because the environment is unlikely to provide resources in the precise proportions required, at any given site a plant should be limited by the single resource in lowest supply relative to need. A plant should increase growth in response to addition of its one limiting resource until it becomes limited by some other resource.*" This proposal suggests an extremely low elasticity of substitution between functions, such that equation (7) would be $E = \min\{E_1, \ldots, E_G\}$.

Connection to Weitzman (1998)'s *Noah's Ark*. In Appendix C.2, we provide an explicit mapping between our framework and the value of biodiversity in Weitzman (1998)'s seminal study on how to prioritize species when preservation is costly. While Weitzman (1998) values species in terms of the distinctiveness of their genetic content, our ecologically-founded framework explicitly focuses on species' heterogeneous contributions to ecosystem services, consistent with arguments in Brock and Xepapadeas (2003) and Polasky, Solow and Broadus (1993) that the economic value of a species need not be related to its contribution to genetic diversity. Our framework allows for more tractable aggregation and can be mapped directly to standard economic objects measuring substitutability and complementarity between species and functions. As a result, it demonstrates clearly how different species' ecological and economic values across ecosystems depend on key parameters such as the distribution of species richness across functions and the elasticities of substitution σ and ϵ_g.

2 Biodiversity and Ecosystem Functioning

Our goal is to study how biodiversity, defined as the number of species in each function S_g, affects the productivity of the overall ecosystem as well as economic output. In this section, we start by examining how E depends on biodiversity, before turning to output effects in Section 3.

2.1 The Effect of Species Loss on Aggregate Ecosystem Services

Combining equations (5) and (7), the production of aggregate ecosystem services is:

$$E = \left[\sum_{g=1}^{G} \bar{E}_g^{\frac{\sigma-1}{\sigma}} s_g^{\phi_g \frac{\sigma-1}{\sigma}} \right]^{\frac{\sigma}{\sigma-1}}. \tag{8}$$

Proposition 1 describes the marginal effect of species loss on aggregate ecosystem services. Formally, we consider the semi-elasticity of aggregate ecosystem services E to a species shock dS_g, consistent with the idea that extinction risk is at the species level and does not scale with the number of species left. In other words, the relevant incremental shock in an ecosystem function reduced to only 3 species remains the loss of a whole species, and not a small fractional loss (e.g., 0.3 species). Note that this Proposition, like the remainder of the paper, assumes that $\sigma < 1$ and $\phi_g < 1$, motivated by the previous section.

Proposition 1. *E is increasing in each S_g, with marginal effects (or, more formally, semi-elasticity) given by:*

$$\frac{\partial \log E}{\partial S_g} = \frac{\phi_g}{S_g} \left(\frac{E_g}{E} \right)^{\frac{\sigma-1}{\sigma}} > 0. \tag{9}$$

The marginal effect of a species shock dS_g on ecosystem service production is:

(i) Decreasing in S_g, so that aggregate ecosystem service provision E is concave in S_g (while Equation (9) shows the concavity of $\log E$ with respect to S_g, the proof shows that E itself is also concave in S_g);

(ii) Decreasing in E_g/E, so that species loss in relatively scarcer functions has a stronger effect on E;

(iii) Decreasing in the substitutability and the degree of competition between species, both of which reduce ϕ_g.

Abundant Functions. *A species shock dS_g does not affect the aggregate provision of ecosystem services if:*

(i) Function g is abundantly provided, i.e., $E_g \to \infty$; or

(ii) Holding E_g fixed, the number of species providing function g is large, i.e., $S_g \to \infty$.

Critical Functions. *The effect of a species shock dS_g becomes infinitely large as $s_g = S_g/\bar{S}_g \to 0$:*

$$\lim_{S_g/\bar{S}_g \to 0} \frac{\partial \log E}{\partial S_g} = \infty. \tag{10}$$

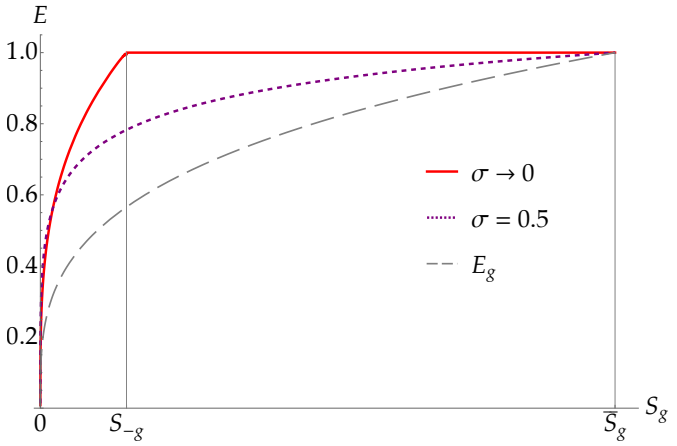
Discussion. Proposition 1 highlights the concavity of E with respect to S_g, which reflects the compounding of the concavity of the within-function and across-function relationships described in the previous section. When species loss occurs in a function with a high stock of biodiversity, or in a function that is not constraining the production of aggregate ecosystem services, this loss has only small effects on the total ecosystem service production. On the other hand, as biodiversity gets depleted, and the number of species collapses to zero, the negative effects of further biodiversity losses become large.

Figure 3 shows a calibrated example of the function-level concavity (dashed line, similar to Figure 2) as well as the additional concavity in the relationship between the aggregate E and S_g (solid lines, corresponding to different calibrations for σ). In this example, the maximal initial number of species per function is $\bar{S} = 100$, but all functions other than g have already suffered species loss, bringing S_{-g} to 15 (where S_{-g} refers to all $j \neq g$). Even after species loss in function g has started to reduce E_g, this will only affect overall ecosystem productivity E once function g becomes sufficiently limiting for the ecosystem as a whole. This intuition is most transparent when considering the case of extreme complementarity ($\sigma \to 0$), which corresponds to a Leontief aggregator $E = \min\{E_1, ..., E_G\}$, shown as a red line. In that case, the production of aggregate ecosystem services becomes entirely determined by the function with the smallest number of species. Consequently, biodiversity-loss-induced changes in E_g have no impact on E until g becomes the limiting function, which happens once S_g falls below $S_{-g} = 15$.

A first implication of the concavity of E with respect to S_g is that we cannot extrapolate any observed small effects of past initial species losses on ecosystem service provision (and economic output) to understand what will happen as S_g continues to decline. Instead, the concavity highlights that a key consequence of past biodiversity losses is that they make *future* damages from biodiversity losses more severe, and that a small economic impact today may thus be hiding a large exposure to further losses. Indeed, Figure 3 shows that our ecologically-founded modeling approach generates the presence of non-linearities and "tipping points" in the relationship between biodiversity and ecosystem service production, the absence of which from existing models has been lamented by researchers studying the economic effects of biodiversity loss (e.g., Svartzman et al., 2021).

A second implication of the concavity of E with respect to S_g is that the the marginal effect of species loss on the productivity of the overall ecosystem becomes high (or even infinite) as $s_g \to 0$. In other words, as the number of species in a function declines, the remaining species are likely to become *keystone species*, defined as "*species whose impact on its community or ecosystem is large, and disproportionately large relative to its abundance*" (Power et al., 1996). This is because few other species remain to fulfill the same function combined with the difficulty of substituting across functions in the production of

Figure 3: Ecosystem Service Production and Biodiversity



Note: Figure shows E and E_g as functions of S_g for two values of σ, with $\bar{E}_{-g} = \bar{E}_g$ and $S_{-g} = 15$, normalizing $E = 1$ and $E_g = 1$ when $S_g = \bar{S}_g = 100$.

aggregate ecosystem services. This conclusion is consistent with empirical evidence that past losses of keystone species have had meaningful ecological and economic effects. For example, Frank and Sudarshan (2024) find large social costs from the collapse of the vulture population in India, which led, among other things, to a 4% increase in mortality due to a decline in sanitation services. The authors emphasize that in the relevant ecosystems, vultures were without a "*good functional replacement in the ecosystem.*"

More generally, Proposition 1 highlights that the effect on ecosystem productivity of losing a species is context-dependent: losing species in a group that constrains overall ecosystem output and where there is little remaining functional redundancy can have large effects, while losing species in the same ecosystem but in a group with more remaining functionally similar species (or one that does not constrain aggregate ecosystem productivity) has much smaller effects. This result aligns closely with an ecology literature that finds that "*ecosystem response to extinction or invasion in the real world will be determined at least as much by which species and functional traits are lost and remain behind as by how many species are lost. [...]*" (Hooper et al., 2005). The relative impact of species loss in two functions g and h on ecosystem services can be formally captured by their marginal rate of substitution:

$$\text{MRS}_{g,h} = \frac{\partial E/\partial S_g}{\partial E/\partial S_h} = \overline{\text{MRS}}_{g,h} \frac{s_g^{-\left[1+\phi_g\left(\frac{1}{\sigma}-1\right)\right]}}{s_h^{-\left[1+\phi_h\left(\frac{1}{\sigma}-1\right)\right]}}, \tag{11}$$

where $\overline{\text{MRS}}_{g,h} = \phi_g/\phi_h \left(\bar{E}_g/\bar{E}_h\right)^{1-1/\sigma}$ is the marginal rate of substitution absent biodiversity loss in functions g and h, i.e., when $s_g = s_h = 1$. Equation (11) describes the relative loss of aggregate ecosystem output from losing species across two functional groups. The two sources of concavity in the model, captured by $\phi_g < 1$ and $\sigma < 1$, interact to determine the relative cost of losing species across different functions.

The MRS between different species provide a framework to guide which conservation activities should be required to offset a certain ecosystem loss. Such *biodiversity offsets*, defined by Carbon Brief as "*conservation activities intended to compensate for the lasting impacts of development on species and ecosystems that persist even after other mitigation measures,*" are an important component of environmental regula-

tion in many jurisdictions, including in Australia, Great Britain, the European Union, and the United States. A key principle of biodiversity offsets is that they should lead to a "no net loss" outcome. Our findings highlight the importance of specifying the exact metric for "no net loss" given that "no net loss of species" or "no net loss of wetlands" does not generally translate into a "no net loss for ecosystem functioning."

2.2 Biodiversity Shocks and the Fragility of Ecosystem Services

Proposition 1 above highlights the highly non-linear effect of species loss on the production of ecosystem services, focusing on species loss in a single function g. We now extend this analysis to characterize how the aggregate impact of an *arbitrary distribution of species losses across multiple functions* depends on the current, multi-dimensional, state of biodiversity in each function. Throughout this section, we simplify expressions by assuming that $\bar{n}_g$ and $\bar{S}_g$ are the same across functions.

We denote the current state of biodiversity in each function as s_g, and consider a loss of in biodiversity in several functions, given by the vector $d\boldsymbol{s}$; in the Appendix, we extend this result to additionally allow for shocks to species abundances holding the number of species fixed. Proposition 2 decomposes the aggregate effect of a shock to biodiversity $d\boldsymbol{s}$ into three conceptually distinct parts.

Proposition 2. *Given the state of biodiversity $\boldsymbol{s} = \{s_g\}_{g=1,\dots,G}$, the effect of shocks to species $d\boldsymbol{s} = \{ds_g\}_{g=1,\dots,G}$ on aggregate ecosystem service provision E is given by:*

$$d\log E = \underbrace{\sum_{g=1}^{G} \frac{\omega_g \alpha_g}{s_g} ds_g}_{\Delta \text{ Community abundance}} + \underbrace{\sum_{g=1}^{G} \frac{\omega_g}{s_g(\epsilon_g - 1)} ds_g}_{\Delta \text{ Within-function niche differentiation}} + \underbrace{Cov\left[\gamma_g, \frac{\phi_g}{s_g} ds_g\right]}_{\Delta \text{ Across-function imbalances in biodiversity}}, \tag{12}$$

where we denote:

$$\begin{aligned}
\omega_g &= \frac{N_g}{\sum_{j=1}^{G} N_j} && \textit{(abundance weights)},\\
\mu_g &= \frac{\partial \log E}{\partial \log E_g} = \frac{s_g^{\phi_g \frac{\sigma-1}{\sigma}}}{\sum_{j=1}^{G} s_j^{\phi_j \frac{\sigma-1}{\sigma}}} && \textit{(criticality weights)},\\
\gamma_g &= \mu_g - \omega_g && \textit{(criticality-abundance gap)}.
\end{aligned}$$

In particular, the impact of a common species loss shock $ds_g = ds, \forall g$, is

$$d\log E = \mathcal{F}(\boldsymbol{s}) ds, \tag{13}$$

where the ***fragility of ecosystem services****, or simply fragility, is denoted by*

$$\begin{aligned}
\mathcal{F}(\boldsymbol{s}) &= \sum_{g=1}^{G} \mu_g \frac{\phi_g}{s_g} \\
&= \sum_{g=1}^{G} \frac{\omega_g \alpha_g}{s_g} + \sum_{g=1}^{G} \frac{\omega_g}{s_g(\epsilon_g - 1)} + Cov\left[\gamma_g, \frac{\phi_g}{s_g}\right].
\end{aligned} \tag{14}$$

Before providing intuition for the Proposition, we describe some of the elements that appear in it. The *abundance weights* ω_g are the population shares of each function in the overall ecosystem, and thus sum to 1. Abundance weights do not depend on elasticities of substitution (σ or ϵ_g), and, all else equal, function g's population share increases with s_g, since more species directly implies more biomass.

The *criticality weights* $\mu_g = {}^{\partial \log E}/_{\partial \log E_g}$ measure the marginal contribution of each function expressed in terms of biodiversity $\{s_g\}$. These weights also sum to 1, mirroring factor shares in standard growth accounting.[13] In the Cobb-Douglas limit $\sigma \to 1$, all the μ_g would be constant equal to $1/N$, just like factor shares are constant with Cobb-Douglas production functions. With σ strictly below 1, as we assume, these marginal contribution shares depend on the distribution of biodiversity $\{s_g\}$. A function g's criticality weight μ_g is decreasing in its own function's biodiversity s_g: functions become more critical when biodiversity is degraded. For two functions g, h sharing the same exponent ϕ, function g is more critical if and only if it has suffered larger past species losses ($s_g < s_h$). For two functions with the same past biodiversity losses ($s_g = s_h$), the function with the lower ϕ is more critical. In addition, higher complementarity across functions (lower σ) magnifies differences in criticality induced by variations in biodiversity s_g. Conceptually, the relative criticality of two functions g, h is related to the marginal rate of substitution between two species in these functions, defined in Section 2.1: ${}^{\mu_g}/_{\mu_h} = {}^{s_h}/_{s_g} \times \text{MRS}_{g,h}$.

Finally, the *criticality-abundance gap* $\gamma_g = \mu_g - \omega_g$ captures the difference between function g's marginal contribution to the production of aggregate ecosystem services and its population share. It is positive if and only if function g contributes more productively to aggregate ecosystem services at the margin than its population share. A positive gap can happen because ϕ_g is relatively high (e.g., due to stronger niche differentiation effects in function g) or because biodiversity s_g in that function is particularly low. By construction, the gaps γ_g always sum to 0, and, in general, some are positive and some negative. They are all equal to 0 only in the case of uniform past biodiversity losses ($s_g = s$ for all g). A lower σ amplifies the absolute magnitude of both positive and negative gaps.

Decomposing the Effects of Biodiversity Loss. Proposition 2 shows that the total effect of species loss on ecosystem service production can be decomposed into three distinct channels. The most obvious is the direct change in community abundance captured by the first term in equation (12): $\sum_{g=1}^{G} {}^{(\omega_g \alpha_g)}/_{s_g} ds_g$. Species loss leads to a decline in the total mass of "producers," thereby reducing total ecosystem service production. The community-abundance effect of the initial species loss is partly offset, however, by compensatory growth of the remaining species. The larger the within-function competition for resources (lower α), the more the extinction of some species benefits the surviving ones. In the extreme case of full compensatory growth ($\alpha = 0$), total abundance is completely unaffected by species loss. Crucially, this first effect is unrelated to bio*diversity*, and would be present even if ecosystem services were produced by a single, homogeneous, species, or equivalently, if all species across all functions were perfectly substitutable (i.e., if $\epsilon_g = \sigma = \infty$).[14] By contrast, the other terms in equation (12) can be non-zero only if there is a value of biodiversity in the sense that not all species and functions are perfect substitutes.

The second term, $\sum_{g=1}^{G} {}^{\omega_g}/_{s_g(\epsilon_g - 1)} ds_g$, denotes the effects from changes in within-function niche dif-

[13] For instance, with a production function $Y(L, \dots)$ where L is labor priced at a competitive wage $w = {}^{\partial Y}/_{\partial L}$, the labor share is equal to ${}^{wL}/_{Y} = {}^{\partial \log Y}/_{\partial \log L}$.

[14] As we discuss in the appendix, this term also corresponds to the loss in ecosystem service production that would occur if all species saw a proportional reduction in abundance and there was no species loss.

ferentiation discussed in Section 1.2.1: since a function with fewer species is less effective at extracting all available resources, species loss will lead to a decline in the productivity of a function. When biodiversity in a function has been depleted more (low s_g), further biodiversity losses in that function have larger negative effects on the ability to extract all resources and therefore lead to bigger losses in ecosystem productivity. These effects are bigger in functions with less substitutability across species (low ϵ_g) and disappear if $\epsilon_g \to \infty$ for all g, that is, if species are perfect substitutes within each function.

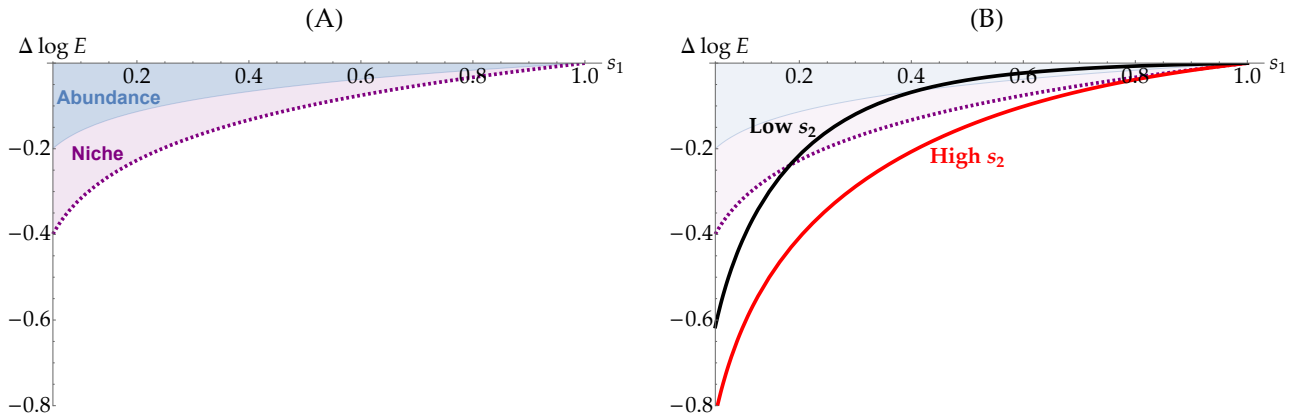
The final term, $\text{Cov}\left[\gamma_g, \phi_g/_{s_g} ds_g\right]$, captures how *imbalances in biodiversity* across functions are affected by shocks to biodiversity. This covariance term is equal to zero if species losses occur around a symmetric initial allocation of speices across functions ($s_g = s$), in which case $\gamma_g = 0$. If instead there are pre-existing imbalances in s_g and the initial allocation of species was thus 'inefficient,' the covariance term can be non-zero.[15] New biodiversity losses have stronger effects than suggested by naive abundance-based measures when they disproportionately hit functions with a higher abundance-criticality gap ($\text{Cov}\left[\gamma_g, \phi_g/_{s_g} ds_g\right] < 0$). Conversely, the losses induce smaller reductions in ecosystem services than suggested by a naive abundance-based measure if they occur in functions that are less critical relative to their abundance ($\text{Cov}\left[\gamma_g, \phi_g/_{s_g} ds_g\right] > 0$). Crucially, even in that case the net effect of species losses when summing up the three terms in equation (12) is still negative, but a simple abundance-based measure that considers only the first term—or even a more sophisticated measure that also accounts for niche differentiation effects in the second term—overestimates the reduction in ecosystem services.

Once again, the intuition is clearest in the limit of no substitution between functions ($\sigma \to 0$). In that case, if new species loss occurs in any function except the most critical one, aggregate ecosystem services E remain unchanged in spite of the fall in total abundance and the decline in niche differentiation. According to our decomposition in equation (12), this means that the third term offsets exactly the first two terms capturing abundance loss and decreased niche differentiation. More generally, the covariance term is larger in absolute value when functions are highly complementary (small σ), in which case the same differences in biodiversity loss across species lead to larger absolute differences in criticality.

Effects of Biodiversity Loss — Numerical Example. Figure 4 provides a graphical intuition behind the decomposition in equation (12). The horizontal axis s_1 captures species loss in one function $g = 1$ starting from $s_1 = 1$, holding other functions intact. Panel A shows the cumulative reduction in ecosystem services relative to the initial condition $s_1 = 1$ due to the first two terms in (12), that is, ignoring any effect of cross-functional imbalances. Equivalently, this is the actual reduction in E that would occur if all ecosystem functions were perfectly substitutable ($\sigma \to \infty$). The blue region labeled "Abundance" captures the reduction in ecosystem services due to the direct effect of lower abundance, whereas the purple region labeled "Niche" captures the loss due to decreased niche differentiation. In

[15] Our prior discussion of marginal rates of substitution in Section 2.1 shows that with such 'inefficient' allocation of biodiversity, productivity E could be improved by 'reallocating' species from less critical functions to more critical ones. This is similar to the literature on the aggregate implications of misallocation of inputs across firms and sectors (e.g., Hsieh and Klenow, 2009; Baqaee and Farhi, 2019*b*). In our setting, the change in imbalances appears as a first-order effect (e.g., as in Baqaee and Farhi, 2019*b*; Bigio and La'O, 2020), which contrasts with the case of "efficient" production networks, in which changes in allocative efficiency and elasticities of substitution only become relevant at the second order (Baqaee and Farhi, 2019*a*). The reason is that Hulten's theorem applies to efficient economies in which firms are competitive profit-maximizers that face no distortions such as taxes or financial frictions. Here we have instead a highly inefficient production structure because biodiversity losses are not the outcome of a profit-maximization problem.

Figure 4: Decomposing the Effect of Species Loss



Note: Panel A shows the cumulated first two terms in equation (12) for s_1 between 0 and 1. The blue region ("Abundance") corresponds to the first term due to changes in abundance and the purple region ("Niche") to the second term due to changes in niche differentiation. Panel B shows the cumulated total change, holding the first two terms constant. The solid black line ("Low s_2") holds biodiversity in other functions s_2 fixed at a low value and the solid red line ("High s_2") holds s_2 fixed at at 1.

this numerical example, we set $\sigma = 0.1$, $\phi_g = 0.3$, with $\alpha_g = 0.15$ and ϵ_g such that the gains from variety within function $g = 1$ are also equal to $1/(\epsilon_g - 1) = 0.15$ (i.e., $\epsilon_g \approx 7.7$). This example highlights how niche differentiation effects can magnify any direct effect of abundance loss on ecosystem services.

Panel B shows the cumulative reduction in ecosystem services taking into account all three channels in equation (12). We hold the abundance and niche-differentiation effects fixed, hence the dashed purple line is the same as in Panel A. We highlight the role of cross-functional imbalances by showing how E declines under two scenarios: one where the biodiversity in unaffected functions is high, fixed at $s_2 = 1$ (solid red line labeled "High s_2"), and one where it is already low initially, fixed at $s_2 = 0.4$ (solid black line labeled "Low s_2"). In both cases, we show the change relative to a baseline level when $s_1 = 1$, but the baseline level is itself lower when other functions are already depleted (low s_2).

When s_2 is high, there are no pre-existing imbalances in biodiversity across functions. As we move along the horizontal axis, species loss always affects the most depleted function $g = 1$. As a result, the third term in equation (12) is always negative, and overall ecosystem services decline by more than implied by the abundance and niche differentiation effects. In the Figure, the gap between the solid red line and the dashed purple line captures the cumulative third term in equation (12) due to increased imbalances between functions as more species disappear in function $g = 1$.

When s_2 is low, as depicted on the solid black line, there are pre-existing imbalances in biodiversity in the sense that function $g = 1$ is initially relatively abundant. Therefore, starting from high values of s_1, the actual reduction in E due to species loss in function $g = 1$ is much smaller than implied by abundance and niche differentiation effects: while species loss reduces the abundance and niche differentiation in function $g = 1$, that function does not meaningfully constrain the ecosystem, and thus total losses of ecosystem service production will be small. In this case, naive abundance-based measures—the first two terms in equation (12)—would overestimate the impact on ecosystem services because the covariance term $\text{Cov}\left[\gamma_g, \phi_g / s_g ds_g\right]$ is actually positive. However, once species losses in function 1 have accumulated and function $g = 1$ becomes relatively depleted relative to the other functions, the black

line crosses the purple dashed line, which means that naive abundance-based measures now *underestimate* the actual reduction in ecosystem services, as the covariance term turns negative and thus reinforces the direct loss in abundance and niche differentiation.

The Fragility of Ecosystem Services. The second half of Proposition 2 considers the effects of biodiversity losses from a shock that affects species in all functions equally (so $ds_g = ds$ for all g). This special case allows us to introduce the notion of *fragility* of ecosystem services $\mathcal{F}(\boldsymbol{s})$, which captures the decline in the production of aggregate ecosystem services following such a common shock. Moreover, if that common shock ds is stochastic, fragility captures a notion of the ecosystem's *exposure to biodiversity risk*.

Fragility is also determined by the three forces identified in Proposition 2 and thus depends on the *asymmetry* in past species losses. To illustrate the importance of this asymmetry, consider as a minimal example the case of two functions ($G = 2$), with $\phi_1 = \phi_2 = \phi$ and potentially different initial levels of biodiversity, say $s_1 \leq s_2$. To focus on cross-functional effects in this example, we abstract from within-function niche differentiation and let $\epsilon_g \to \infty$, which drops the second of the three terms in equation (12). Then fragility can be expressed as:

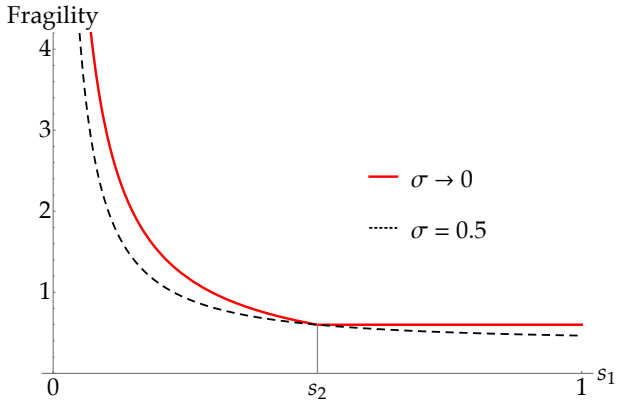
$$\mathcal{F}(\boldsymbol{s}) = \phi \left[\frac{\mu_1}{s_1} + \frac{1-\mu_1}{s_2} \right] = \underbrace{\phi \left[\frac{\omega_1}{s_1} + \frac{1-\omega_1}{s_2} \right]}_{\Delta \text{ Community abundance}} + \underbrace{\phi \gamma_1 \left[\frac{1}{s_1} - \frac{1}{s_2} \right]}_{\Delta \text{ Imbalances}}.$$

Both terms are always positive, with the second term equal to zero if and only if initial conditions are symmetric, $s_1 = s_2$: imbalances always increase ecosystem fragility and thus add to overall loss of ecosystem services in response to a common shock (this contrasts with the case of asymmetric species loss which might "even things out" by hurting disproportionately less depleted functions).

Figure 5 shows $\mathcal{F}$ as a function of s_1 (holding s_2 fixed at 0.5) for different values of σ. More complementarity across functions (lower σ) amplifies the fragility of ecosystem services for any value of $s_1 \neq s_2$ through the imbalances term, because a lower σ raises the criticality of the less abundant function and thus increases the criticality-abundance gap, γ_1. Species losses in function $g = 1$ reduce abundances in that function and through this channel always raise fragility. When we lose species, the contribution of changes in the second term to changes in fragility can be positive or negative. In particular, in the region $s_1 > s_2$, losses in function $g = 1$ reduce dispersion in s and thus the term due to imbalances. However, despite these two opposing forces when $s_1 > s_2$, the net effect is that a lower s_1 always (weakly) increases fragility. In the limit case of no substitutability between functions ($\sigma \to 0$), fragility is entirely determined by the *most critical* function: $\mathcal{F}(\boldsymbol{s}) \to \frac{\phi}{\min_g s_g}$. In that case, Figure 5 has a kink at $s_1 = s_2 = 0.5$ with $\mathcal{F}$ constant and equal to ϕ/s_2 for $s_1 > 0.5$.

Over time, as natural and human-made shocks affect the stock of biodiversity $\boldsymbol{s}$, the fragility of the ecosystem—and, thus, the ecological and economic risks associated to further losses—varies. In Appendix C.3, we show that the accumulation of random species losses over time tends to produce an increase in ecosystem fragility, because each additional shock to biodiversity tends to increase the imbalance in biodiversity degradation across functions. Naturally, a if species loss over time tends to cluster in a subset of functions, this leads to additional increases in fragility over time.

Figure 5: The Fragility of Ecosystem Services.



Note: Figure shows $\mathcal{F}$ as a function of s_1, fixing $s_2 = 0.5$ and $\phi = 0.3$ for $g = 1, 2$. Lines corresponds to different values of σ.

2.3 Measuring Fragility

As discussed, the concept of ecosystem fragility is useful to characterize the exposure of ecosystems to biodiversity risk. In this section, we propose and implement an approach to measuring fragility.

In a first step, we derive a first-order approximation to express fragility as a function of two properties of the ecosystem that can be observed in the data (see Appendix B.2 for details): the *average* and the *dispersion* of species losses across different functions. To simplify expressions, suppose that the only heterogeneity between functions is the extent of past losses, and thus the parameters α_g, ϵ_g, and ϕ_g are the same across functions. Denote $\bar{s} = \mathrm{E}[s_g]$ the average share of surviving species and let $s_g = \bar{s}(1 + \delta_g)$, so that δ_g is function g's deviation from the average. Fragility can then be approximated as:

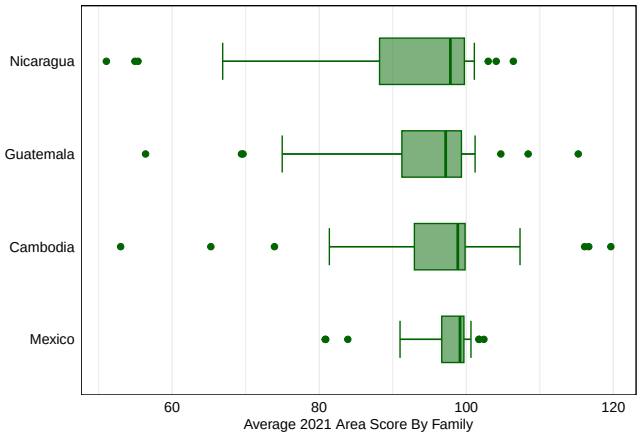
$$\mathcal{F}(\boldsymbol{s}) \approx \frac{\phi}{\bar{s}} \times \left\{ 1 + \left[1 - \phi + \frac{\phi}{\sigma} \right] \mathrm{Var}(\delta_g) \right\}, \tag{15}$$

where $\mathrm{Var}(\delta_g) = \sum_g \delta_g^2$. The term $\phi/\bar{s}$ is the only source of fragility if losses are the same for all functions (i.e., if $s_g = \bar{s}$ for all g). However, the term in brackets illustrates that, conditional on average species loss $\bar{s}$, dispersion in species loss captured by $\mathrm{Var}(\delta_g)$ further amplifies fragility. Dispersion has a stronger impact if σ is lower, that is, if different ecosystem functions are less substitutable.

In a second step, we measure the average species loss and its dispersion across functions. To measure the population health of different species, we work with the *Map of Life* database of Jetz, McPherson and Guralnick (2012). This data provides country-level area scores calculated annually between 2001 and 2021 for a large number of species of terrestrial vertebrates (see Appendix A). Area scores measure a species' habitat-suitable range in the country as a percentage of that range in 2001. These area scores serve as good proxies for relative species abundance, since habitat loss generally reduces species abundance and increases extinction risk (Newbold et al., 2015; Powers and Jetz, 2019). While this data allows us to measure habitat loss for terrestrial vertebrates—which include birds, amphibians, mammals and reptiles—we do not observe species health for marine life, invertebrates, and plants.

To group species by ecosystem function, we obtain taxonomic classifications from the *TetrapodTraits* data of Moura et al. (2024). We observe the order, suborder, and family of each species, which correspond

Figure 6: Area Score by Family for Selected Countries in 2021



Note: Boxplot of average 2021 family-level area scores for Nicaragua, Guatemala, Cambodia, and Mexico. Area scores measure a species' habitat-suitable range as a percentage of its range in 2001. An area score of 100 represents no change in habitat size between 2001 and 2021. Family-level data represents unweighted means across reported species in that family. The whiskers indicate the 5th and 95th percentiles, while the dots mark the highest and lowest 3 data points for family-level area scores.

to progressively finer taxonomic ranks based on both evolutionary relationships and conventionally-defined groupings of functional and genetic similarity. Species within the same taxonomic group often perform similar ecosystem functions, as these factors—evolutionary, functional, and genetic—are closely intertwined in shaping species' ecological roles (Webb et al., 2002; Safi et al., 2011).

Combining these datasets yields species-level health proxies and functional classifications for over 2 million species-country-years covering 221 countries and territories. In 2021, we observe 446 species in the average country, distributed across an average of 82 families, 33 suborders, and 27 orders.

Figure 6 shows the distribution of 2021 family-level average area scores across countries with different levels of average habitat loss: in Mexico and Cambodia, the habitat range for an average species family was only 2–4% smaller than in 2001. In contrast, in Guatemala and Nicaragua, the habitat range for an average family had shrunk by 6–8%. Within countries with similar average habitat loss, the variation in this loss across families can differ widely. At the 10th percentile, habitat area by family has declined by 26% in Nicaragua, compared to 18% in Guatemala. One example of a family that has suffered significant habitat loss in Nicaragua is the *Atelidae* family, with a 36% decline in habitat between 2001 and 2021. This family includes species such as the Nicaraguan Spider Monkey, whose endangered status is largely due to this habitat loss (Cortes-Ortìz et al., 2020). Because these species play a crucial role in seed dispersal, their decline threatens the plant population dynamics necessary to maintain ecosystem health. On the flip side, conservation efforts such as reforesting the Pacific Slope to support species like the Ocelot have successfully expanded the *Felidae* family's habitat range by 0.9% since 2001.[16]

[16]Similarly, while Cambodia and Mexico have experienced comparable overall habitat loss, Cambodia shows much greater variability across families. At the 10th percentile, habitat area by family has declined by 13% in Cambodia, compared to 6% in Mexico. One example of a family that has suffered significant habitat loss in Cambodia is the *Hylobatidae* family, with a 35% decline in habitat range between 2001 and 2021. This family includes species such as the Northern Yellow-Cheeked Gibbon, whose endangered status is attributed to this habitat loss (IUCN, 2020). These species play a crucial role in seed dispersal within Southeast Asian forests, and their decline threatens ecosystem stability. In contrast, conservation efforts targeted at the near-extinct Hog Deer have increased the habitat of the *Cervidae* family by 8%.

3 Biodiversity and the Economy

In this section, we embed the production function for ecosystem services introduced above in an integrated model of the economy and nature. We first add structure to equation (1) and specify an aggregate production function that includes physical capital, land use, and ecosystem services. We then provide empirical evidence from asset prices that suggests biodiversity losses and ecosystem fragility do indeed affect economic activity. In the subsequent section we build in this work to study the optimal use of ecological resources that accounts for the feedback between economic activity and biodiversity.

3.1 Ecosystem Services as a Factor of Production

We specialize equation (1) to the following economic production function, which could easily be expanded to include labor and other factors of production:

$$F(K, E, uL) = \left(\left[K^{\theta} (uL)^{1-\theta} \right]^{\frac{\xi-1}{\xi}} + a_E E^{\frac{\xi-1}{\xi}} \right)^{\frac{\xi}{\xi-1}}. \tag{16}$$

Output is produced from aggregate ecosystem services E and a composite of capital (K) and land (uL), with θ denoting the share of capital among the factors unrelated to nature. We refer to L as the (fixed) amount of land available; $u \in [0, 1]$ is a choice variable, that captures the fraction of land used for economic production, so that $1 - u$ is the land that is left to nature. In Section 4, we then specify the process through which increases in u lead to reductions in natural capital and biodiversity.

Strong vs. weak sustainability. The production function in equation (16) could feature substitutability or complementarity between ecosystem services and other types of capital, depending on the value of ξ. While most of the analysis of the model below holds in both cases, we highlight throughout the implications of the so-called "strong sustainability" hypothesis, corresponding to $\xi < 1$. This concept, proposed by Dietz and Neumayer (2007) and Ekins et al. (2003), highlights the difficulties of substituting for several key ecosystem services by increasing other factors of production. This insight was core to the influential Dasgupta (2021) review, which concluded that there is "*little-to-no substitution possibilities between key forms of natural capital and produced capital, or for that matter any other form of capital.*"[17]

The strong sustainability hypothesis has direct implications for how the importance of biodiversity varies as economies accumulate capital. Denoting composite capital as $\tilde{K} = K^{\theta}(uL)^{1-\theta}$, the cross-derivative of log-output with respect to the two factors of production $\tilde{K}$ and E is:

$$\frac{\partial^2 \log F}{\partial \tilde{K} \partial E} = \left(\frac{1}{\xi} - 1 \right) \frac{a_E E^{\frac{1}{\xi}} \tilde{K}^{\frac{1}{\xi}}}{(\tilde{K} E^{\frac{1}{\xi}} + a_E E \tilde{K}^{\frac{1}{\xi}})^2}, \tag{17}$$

[17] In a lengthy review of the substitutability of ecosystem services and other factors of production, Ayres (2007) similarly comments that "*the surprise, for me, in writing this paper is the extent to which the biosphere embodies a fundamental natural technology for which there is no known (or likely) alternative and which is truly essential to human survival. That is the technology for reducing carbon dioxide and recombining the carbon with hydrogen and other elements. This technology took hundreds of millions of years to evolve. So far as we now know, only photo-synthetic organisms can do that, and only with the help of organic compounds containing phosphorus.*" And even if some ecosystem services such as water filtration already have some substitutability with physical capital, it is possible to view our analysis of aggregate ecosystem services as corresponding only to the remaining non-substitutable ecosystem services, while those that are highly substitutable with physical capital could be considered as just another easily replaceable factor of production.

which is positive under strong sustainability ($\xi < 1$) and negative otherwise ($\xi > 1$, also known as "weak sustainability"). Under strong sustainability, the marginal importance of ecosystem services in production ($\partial logF/\partial E$) becomes larger as the other factors of production grow. Intuitively, in a capital-rich economy, ecosystem services tend to be the constraining factor and biodiversity loss is particularly damaging. Our empirical analysis in the next section shows that, consistent with the predictions of strong sustainability, proxies for economic risks from biodiversity loss are higher in countries with a lower ratio of natural capital to other factors of production.

3.2 Biodiversity and the Economy: Evidence from Asset Prices

We now present empirical tests of some of the key implications of the model that relate biodiversity loss to economic activity. Several factors complicate this analysis. First, changes in biodiversity are slow moving and economic output is only observed at low frequencies, which makes identifying a causal relationship between these aggregate quantities challenging. Second, as highlighted by our model, a lack of relationship between biodiversity loss and current output does not by itself imply that there are no meaningful economic effects due to biodiversity loss: instead, even without a large current effect, current losses might have made the economy more fragile and thus more exposed to *future* losses.

We therefore take an alternative approach, and explore whether *asset prices* respond to *news* about biodiversity loss. Focusing on asset prices rather than measures of current economic output has two advantages. First, asset prices reflect the present discounted values of future cash flow as well as their riskiness, and should therefore respond to changes in economic resilience that have not yet translated into changes in output. Second, while economic activity and biodiversity loss move slowly, *news* about current and future biodiversity loss arrives more frequently, and asset prices should reflect such news immediately As a result, researchers have more empirical variation to detect possible relationships.

Concretely, we study the effects of news about biodiversity loss on sovereign credit default swap (CDS) spreads, which capture the cost of insurance against default on government debt and thus reflect expectations of aggregate economic tail-risk probabilities. Conceptually, bad news about biodiversity loss will lead to rising CDS spreads if market participants believe that such biodiversity loss will have negative consequences for countries' economic prospects and thus lead to higher default probabilities. Our model predicts that news about biodiversity losses should affect economic outcomes more for countries that are more exposed to biodiversity shocks: countries whose biodiversity is more degraded on average (Proposition 1), and countries for which the degradation of biodiversity is more uneven across ecosystem functions (Proposition 2). More exposed countries should then see stronger movements in CDS spreads upon arrival of biodiversity news. Biodiversity news should also affect CDS spreads more for countries where ecosystem services are more binding in the production process, for example because other factors are more plentiful. This section provides an empirical test of these predictions.

3.3 Data Description

CDS Spreads. We use CDS pricing information from Markit and include data on all available sovereign CDS of maturities 1, 5, 10, 15, 20 and 30 years. We focus on USD-denominated CDS, though including non-USD-denominated CDS gives similar results. Our main object of interest is the CDS spread, which is the annual fee to purchase protection against a negative credit event, usually quoted as a fraction

of notional amount insured (typically in basis points per year). After merging this CDS data with the measures of biodiversity loss described below, we obtain a sample of 385,861 weekly changes in CDS spreads for 79 distinct countries between 2001 and 2022 (some countries are only observed in some years). Since the level of CDS spreads varies substantially across countries with different credit risk, we measure changes in CDS spreads in percent relative to the prior-week baseline (instead of studying absolute changes). At the 5th percentile of the distribution, CDS spreads fell by 12.1 percent in a week; at the 95th percentile, they increased by 14.9 percent. The 5-year tenor is the most common at 18.9% of the sample, while long maturities of 30 years are the least common at 14.8% of the sample.

Negative Biodiversity News. To measure aggregate news about biodiversity loss, we build on the empirical work of Giglio et al. (2023), who produce a weekly index of news coverage of biodiversity loss in the *New York Times*. Appendix Figure A.1 shows this news series, with positive index values corresponding to weeks with more bad news about biodiversity loss. To isolate the unanticipated component of negative biodiversity news, we construct AR(1) residuals of the index, similar to the approach in Engle et al. (2020) and Alekseev et al. (2022).

Biodiversity Destruction. To measure the state of biodiversity in a country, we work with information from the Environmental Performance Index (EPI) published by the Yale Center for Environmental Law & Policy (Wolf et al., 2022). The EPI provides measures of a country's performance on several environmental aspects. We construct our main measure, *BiodiversityDestructionScore*, by aggregating several indicators related to biodiversity and ecosystem vitality (see Appendix A for details): (i) a measure of changes in biological diversity; (ii) a measure of the amount of suitable habitat remaining for each species; and (iii) measures of tree cover loss, grassland loss, wetland loss, and fisheries loss. Since higher values in the EPI indicators represent better environmental outcomes, we reverse the sign so that larger values correspond to greater biodiversity degradation. Since the *BiodiversityDestructionScore* measures biodiversity destruction relative to a baseline in a given country (instead of comparing absolute biodiversity richness across countries), it aligns well with the metric of biodiversity loss used in the model, $s_g = S_g/\bar{S}_g$, which also captures biodiversity loss relative to the initial number of species present.

The EPI is available as of the year 2022, but also includes a baseline version of the indicator "derived from applying the same methodology to data from approximately 10 years prior to current measurements." In our baseline analysis, we average across measures at both points in time to construct our country-level *BiodiversityDestructionScore*. Appendix Table A.1 shows the *BiodiversityDestructionScore* by country, highlighting substantial variation within and across regions. Worldwide, some of the lowest scores (corresponding to the least biodiversity destruction) are observed in the Middle East. Countries with the highest scores (corresponding to the most biodiversity destruction) span a wide geographic range with Portugal, Uruguay, Malaysia and Ghana ranking at the top. The low scores of many Middle Eastern countries reflect the fact that large swaths of their desert landscapes are still relatively un-eroded and endemic species are in comparatively good shape even though they tend to have lower absolute values of species density than other habitats such as rainforests. There is also substantial local variation between countries with similar natural habitats. For instance, Jordan has one of the lowest biodiversity destruction scores while nearby Lebanon has seen substantially more biodiversity destruction.

Dispersion of Habitat Loss. To measure the dispersion in species loss across ecosystem functions, we follow the approach described in Section 2.3. Specifically, we categorize species into taxonomic families—which proxy for ecosystem functions—using the TetrapodTraits data (Moura et al., 2024). We then use species-level data on relative changes in habitat size between 2001 and 2021 from the Map of Life (Jetz, McPherson and Guralnick, 2012) to obtain average habitat loss by family. We obtain our *AcrossFamilyHabitatLossDispersion* measure by taking the standard deviation of this average habitat loss across families in a country. Appendix Table A.2 shows the across-family dispersion of habitat destruction by country. As discussed in Section 2.3, a large dispersion in habitat destruction can occur in both high- and low-loss countries. This indicates that it is a distinct concept from average losses in biodiversity captured by the *BiodiversityDestructionScore*.[18]

Importance of Natural Capital. To measure the extent to which ecosystem services are the constraining factor in a country's production of output, we use the share of a country's wealth that is not derived from renewable natural capital, *NonNaturalCapitalShare*, where higher values indicate lower abundance of natural capital relative to other factors of production. This measure is based on the World Bank's wealth accounting data and is available through the ND-GAIN database (see Appendix A for details).

In our baseline analysis, we average the share of non-natural capital over the three reporting dates in the ND-GAIN data: 1995, 2000, and 2005. Appendix Table A.6 shows the share of each country's wealth that is not derived from renewable natural capital. On average, non-natural capital accounts for 89% of a country's wealth, though there is substantial variation—from 64.5% at the 5th percentile to 99.2% at the 95th percentile. A high share of non-natural capital can stem from low renewable natural capital or an abundance of other capital. The distribution of *NonNaturalCapitalShare* across countries reflects both these forces. Ghana has one of the lowest shares of non-natural capital in our sample, reflecting both a relatively well-preserved state of biodiversity in the country and lower levels of physical capital due to its low level of economic development. Conversely, some of the highest shares of non-natural capital are observed in the world's wealthiest countries. Singapore, one of the world's richest countries, has the highest share of non-natural capital in our sample despite having comparatively intact nature.

3.4 Empirical Analysis

Specification. To explore the effect of negative news about biodiversity loss on CDS spreads, and to assess whether this sensitivity varies with country characteristics such as the current state of biodiversity, we estimate the following equation:

$$\begin{aligned}\Delta CDS_Spread_{i,m,t} = \alpha &+ \beta_1 BiodiversityNews_t \\ &+ \beta_2 BiodiversityNews_t \times BiodiversityDestructionScore_i \\ &+ \beta_3 BiodiversityNews_t \times AcrossFamilyHabitatLossDispersion_i \\ &+ \beta_4 BiodiversityNews_t \times NonNaturalCapitalShare_i \\ &+ \xi_{i,m,year} + \epsilon_{i,m,t}.\end{aligned} \tag{18}$$

[18] We prefer the *BiodiversityDestructionScore* to the average habitat loss from the Map of Life data as our baseline measure of average biodiversity loss in a country. This is because the EPI data incorporates many more species than the Map of Life data, which only includes information on terrestrial vertebrates.

$\Delta CDS_Spread_{i,m,t}$ is the percentage change in the CDS spread for country i, at maturity m, in week t. We winsorize $\Delta CDS_Spread_{i,m,t}$ at the 1% level for each country to ensure our results are not driven by outliers. $BiodiversityNews_t$ is the unanticipated component of news about biodiversity loss as described above, with higher values representing worse news. We standardize $BiodiversityNews_t$ to have mean 0 and standard deviation 1 over the sample weeks. The variables *BiodiversityDestructionScore*, *AcrossFamilyHabitatLossDispersion*, and *NonNaturalCapitalShare* are also standardized to have mean 0 and standard deviation 1 across countries in our sample, which facilitates comparisons of effect sizes across regressors.[19] In our baseline regression, we include country $\times$ year $\times$ maturity fixed effects. We also double cluster standard errors by week and country to account for the fact that all CDS for a given country over time and all CDS in a given week across countries might be affected by common factors.

Results. Table 1 presents estimates of regression (18). In column 1, we only include the biodiversity news index in addition to country $\times$ year $\times$ maturity fixed effects. This specification identifies the average effect of negative biodiversity news across CDS spreads for all countries. Directionally, a one standard deviation increase in adverse biodiversity news is associated with an average increase in CDS spreads of 0.19 percent, but this estimate of the average effect is not statistically significant. The lack of statistical significance and the modest size of the average effect is perhaps not surprising given that, in the time series, many other forces drive CDS spreads, combined with the fact that biodiversity loss might not be a first-order economic concern for many countries.

Column 2 introduces interactions between biodiversity news and three determinants of countries' biodiversity risk exposures: the biodiversity destruction score, the across-family dispersion of prior habitat destruction, and the wealth-share of non-natural capital. The estimated coefficient on the interaction with the biodiversity destruction score, β_2, suggests that CDS spreads are somewhat more sensitive to negative news about biodiversity loss for countries with higher levels of biodiversity destruction, consistent with the predictions from Proposition 1. In terms of magnitudes, a one standard deviation increase in prior biodiversity destruction in a country raises the impact of a one standard deviation higher level of (negative) biodiversity news on CDS spread changes by 0.076 percentage points. Put differently, a one standard-deviation increase in negative biodiversity news leads to a 0.3 percent larger increase in CDS spreads in a country at the 95th percentile compared to a country at the 5th percentile of *BiodiversityDestructionScore*. Relative to an average CDS spread in our sample of 220 basis points, this corresponds to a differential increase in CDS spreads of about 1 basis point, or about 13

The estimated coefficient on the interaction with across-family dispersion of habitat destruction, β_3, suggests that CDS spreads respond more strongly to negative news in countries where biodiversity loss is more unevenly distributed across ecosystem functions. This supports the notion that concentrated habitat destruction increases ecosystem fragility, as in Proposition 2. A one standard deviation increase in habitat destruction dispersion enhances the effect of negative biodiversity news on CDS spread changes by 0.047 percentage points. The estimate of the interaction with wealth-share of non-natural capital, β_4, shows that CDS spreads react more sensitive to negative biodiversity news in countries with a larger wealth-share of non-natural capital, consistent with the intuition that, in these countries,

[19] Since the ranking of countries on each measure is highly correlated across different years, we only focus on values at one measurement point. In the Appendix, we assess robustness to alternative measurement dates.

Table 1: CDS Spreads and Biodiversity News

	(1)	(2)	(3)	(4)	(5)	(6)	(7)
Biodiversity News	0.189	0.175		0.147	0.175		0.146
	(0.121)	(0.117)		(0.116)	(0.117)		(0.116)
Biodiversity News ×		0.076**	0.074**	0.059**			
Biodiversity Destruction Score		(0.032)	(0.034)	(0.027)			
Biodiversity News ×		0.047***	0.043*	0.045***			
Across-Family Dispersion of Habitat Destruction		(0.013)	(0.022)	(0.016)			
Biodiversity News ×		0.077**	0.082**	0.068*			
Wealth-Share of Non-Natural Capital		(0.037)	(0.038)	(0.037)			
Biodiversity News ×					0.104***	0.104***	0.087***
Biodiversity Risk Exposure					(0.033)	(0.035)	(0.030)
Tenor	All	All	All	All	All	5-Year	5-Year
Country × Year × Tenor FE	x	x	x	x	x	x	x
Week × Tenor FE			x			x	
Observations	385,829	385,829	385,811	73,009	385,829	385,811	73,009

Note: Column 1 shows coefficients of regressing percent changes in CDS spreads on AR(1) innovations of the *Biodiversity News* index by Giglio et al. (2023). To ensure our results are not driven by outliers, we winsorize the weekly percentage changes in CDS spreads within each country by 1% at the top and bottom. Column 2 adds interactions of biodiversity news with *Biodiversity Destruction Score*, *Across Family Habitat Loss Dispersion*, and *Non-Natural Capital Share*. Columns 1–3 pool CDS spreads across maturities (1, 5, 10, 15, 20 and 30 years) and include country-year-tenor fixed effects, with column 3 additionally controlling for week-tenor fixed effects. Column 4 mirrors column 2 but is restricted to 5-year CDS spreads. Columns 5–7 use a *Country Exposure* measure, constructed at the country level from the estimated coefficients in column 2. Column 5 builds on column 1 by adding the interaction of biodiversity news with the *Country Exposure* measure. Column 6 adds week-tenor fixed effects to column 5. Column 7 follows the same specification as column 5 but is restricted to 5-year CDS spreads. Standard errors are in parentheses and are double clustered at both the country and at the week levels. Significance levels: * ($p<0.10$), ** ($p<0.05$), *** ($p<0.01$).

ecosystem services are more likely to be the constraining factor of production. A one standard deviation higher wealth share of non-natural capital raises the impact of a one standard deviation higher negative biodiversity news on CDS spread changes by 0.077 percentage points.

Column 3 adds week × maturity (tenor) fixed effects to capture any factors that may affect CDS spreads of a given maturity in a given week that are common across countries. While these fixed effects absorb the direct effect of biodiversity news on CDS spreads across all countries, the specification still allows us to estimate cross-sectional variation in how negative biodiversity news affects asset prices. The estimated coefficients on biodiversity news and its interaction terms remain stable, indicating that the observed relationships persist even after accounting for week-specific fluctuations in credit risk. Column 4 restricts the sample to 5-year CDS spreads, the most common and liquid tenor in our data. The coefficients remain very similar to those using CDS of all tenors.

Discussion. Our results are consistent with the predictions from the model: while negative biodiversity news does not have a statistically significant effect on CDS spreads for the *average* country, it leads to significant increases in CDS spreads in countries with substantial past biodiversity loss, countries with more uneven past biodiversity loss, and countries in which natural capital makes up a smaller share of total wealth, and where it is thus more likely to be the constraining factor of production. While the magnitude of the effect sizes is modest, the evidence suggests that our ecologically founded measures of ecosystem fragility capture key aspects of the ways in which biodiversity loss affects economic activity.

It is important to note that these findings need not imply, for example, that analysts trading CDS necessarily measure our three exposure indicators. Instead, the observed relationships more likely result from the fact that in countries with more dispersed biodiversity loss across families, past biodiversity losses are already putting more substantial strain on ecosystem services production and thus economic output. To the extent that such economic losses are more broadly covered in the media in those countries, analysts focusing on these countries would naturally pay more attention to news about biodiversity loss.

Consider Malaysia, the country with the second-highest across-family dispersion of biodiversity losses. A recent World Bank and Bank Negara Malaysia (2022) report on nature-related financial risks in Malaysia highlights that "*high levels of economic growth in the last two decades [...] has amplified key drivers of nature and biodiversity loss in Malaysia. These include habitat loss and fragmentation, pollution, unsustainable resource extraction and usage, and climate change*." Stakeholders from academia, government, and NGOs interviewed for the report further expressed "*concerns especially with respect to Malaysian forest management, water pollution and species loss.*" A pressing example of these risks is the increasing frequency and severity of floods. The report notes that "*nature also plays an important role for flood and storm protection, on which more than 5 percent of commercial lending in Malaysia depends*," yet ongoing environmental degradation and climate change have already led to "*the frequency and extremity of flood events [increasing] in Malaysia*." Reflecting the economic impact of these trends, Bank Negara Malaysia (2023) estimates that "*economic losses from floods amounted to 0.13% of annual gross domestic product on average*" in Malaysia between 2008 and 2022, with projections suggesting that "*Malaysia is predicted to lose up to 4.1% of GDP in 2030 based on the impact of a theoretical 1-in-20 year flood.*"

Similarly, consider Portugal, the country with the highest value of the *BiodiversityDestructionScore*. Cantarino (2022) highlights how Portugal's worsening drought conditions, driven in part by inefficiencies in agriculture, have contributed to severe biodiversity losses. Outdated irrigation techniques and unsustainable water management practices have strained ecosystems, with one striking example being the collapse of bee populations, where around "*200,000 of the more than 700,000 hives*" were lost in recent years. In a report by Allianz (2023), the loss of pollination services in Portugal—leading to a 6.5% decrease in agricultural output—would result in a reduction of the country's gross domestic product by 1 billion USD, or 0.4% of its GDP, the largest impact among the several countries examined in the report.

In other words, in countries like Portugal and Malaysia, where the large and asymmetric biodiversity degradation already disrupts key industries, the economic effects of biodiversity loss are already meaningful and visible, making it likely that analysts tracking these countries will incorporate biodiversity-related risks in their financial assessments.

Robustness. In Appendix A, we show that our results are robust to adjustments in the data construction choices. For example, we use several alternative measures of across-function imbalances in biodiversity: measuring dispersion of average area scores across suborders instead of families; considering the 10th percentile or the minimum value of area scores across families; assessing the across-family dispersion of habitat scores instead of area scores; and calculating the dispersion only among species that have a meaningful part of their territory in the country. The results are similar regardless of the measure of imbalance in habitat loss. Similarly, we show that the results are robust to using alternative measures for average biodiversity destruction and for the importance of non-natural capital.

Biodiversity Risk Exposure. The theoretical model and the empirical work just discussed highlight that a country's exposure to biodiversity risk depends on a range of variables, including the average and asymmetry in species loss, and the extent to which aggregate production is constrained by ecosystem services. We next construct a single aggregated measure of a country's total physical biodiversity risk exposure that combines these three measures. Specifically, we combine a country's values for the three components of this exposure, *BiodiversityDestructionScore*, *AcrossFamilyHabitatLossDispersion*, and *NonNaturalCapitalShare*, weighting them based on the regression coefficients in column 2 of Table 1. This measure captures how a country's current level of biodiversity influences the impact of negative biodiversity news on CDS spreads. Appendix Table A.10 reports the resulting *BiodiversityRiskExposure* for each country. The countries with the biggest exposure are Malaysia, Singapore, and Portugal, while some of the least exposed countries are in the Middle East.

Column 5 modifies column 2 by replacing the original interaction terms with an interaction between biodiversity news and *CountryExposure*. The estimates indicate that countries with higher exposure to biodiversity risk, as captured by this measure, experience larger CDS spread reactions to negative biodiversity news. A one standard deviation deviation increase in a country's aggregate exposure to biodiversity risk raises the impact of a one standard deviation increase in negative biodiversity news on CDS spread changes 0.104 percentage points. Put differently, a one standard-deviation increase in negative biodiversity news leads to a 0.4 percent larger increase in CDS spreads in a country at the 95th percentile compared to a country at the 5th percentile of *BiodiversityRiskExposure*. Column 6 builds on column 5 by adding week $\times$ maturity (tenor) fixed effects to control for common factors affecting CDS spreads of a given maturity across countries. Column 7 further modifies column 5 by restricting the sample to 5-year CDS spreads, the most common and liquid tenor in our data. In both cases, the estimated coefficients remain stable, positive, and statistically significant.

4 Optimal Conservation Policies

We next explore the decision to preserve biodiversity from an economic perspective. Specifically, we study the optimal use of land when land use increases current output at the cost of reducing biodiversity.

Setup. We consider a simple two-period model that features both standard investment in physical capital and land use u. Equivalently, the fraction $1-u$ of land that is not used for production can be viewed as an investment in the conservation of natural capital. Given initial conditions $(K_0, \bar{\boldsymbol{n}}_{\boldsymbol{0}}, \boldsymbol{s}_0)$, the country's planner chooses, at time 0, land use u and investment into future capital K_1 to maximize

$$\log(C_0) + \beta \log(C_1),$$

where $C_0 = F(K_0, uL, E_0) - K_1$ and $C_1 = F(K_1, \bar{u}L, E_1(u))$. For simplicity, we assume full depreciation of the initial capital stock K_0, and take long-run (date-1) land use $\bar{u}$ as given.[20]

Land use u increases production at time 0, but at a cost to future ecosystem services E_1. This cost comes from two channels that capture the findings from Liang, Rudik and Zou (2021), who document

[20] Modeling the choice of land use at date 1 separately would complicate the problem without meaningfully affecting the main result. One interpretation is that we solve a problem without commitment, with $\bar{u}$ chosen by future generations.

that "*shocks in economic production [...] led to a significant reduction in species abundance, diversity, and stability.*" First, there is a direct impact of land use on overall abundance. For instance, deforestation reduces the maximal abundance of each species, even holding biodiversity (i.e., the number of species) fixed. We capture this by assuming that each species' abundance is multiplied by a factor $1-u$, that is:

$$\bar{n}_{g,1}(u) = (1-u)\bar{n}_{g,0}. \tag{19}$$

Second, land use negatively affects biodiversity in function g according to the following reduced-form specification (see, for example, IPBES, 2019; Johnson et al., 2021):

$$s_{g,1}(u) = s_{g,0} - \delta u. \tag{20}$$

Therefore, greater land use u induces biodiversity loss δu, with $\delta > 0$. One interpretation is that, as the abundance of each species declines due to land use, the risk of extinction increases. Indeed, the ecology literature has found that "*the smaller the population size of a particular species, the more likely it is to go extinct locally, due to random–stochastic–fluctuations*" (Cleland, 2011).[21] Therefore, future ecosystem services follow:

$$E_1 = \left\{ \sum_g \left[\bar{n}_{g,0}(1-u) \left[s_{g,0} - \delta u \right]^{\phi_g} \right]^{\frac{\sigma-1}{\sigma}} \right\}^{\frac{\sigma}{\sigma-1}}. \tag{21}$$

Land use u appears twice in equation (21), thus reflecting the two channels: (i) land use reduces the maximal abundance $\bar{n}$ of each species in a function holding biodiversity fixed; and (ii) land use has an additional negative effect through inducing species loss. In turn, as discussed in Section 2, species loss affects ecosystem service production through three distinct channels that are captured in equation (21): ϕ determines the net abundance loss above and beyond the one captured by equation (19) as well as the reduction in niche differentiation; and σ captures the effect from cross-functional imbalances.

Model Solution. For any factor $X \in \{K, L, E\}$, we denote $\eta_{X,t} = {}^{\partial \log Y_t}/_{\partial \log X_t}$ the elasticity of date-t output to X_t (except in the Cobb-Douglas case, these elasticities are endogenous objects that need to be determined as part of the optimal solution). The optimality condition with respect to investment in physical capital K_1 can be expressed as an optimal savings rate:

$$\rho^* = \frac{K_1}{Y_0} = \frac{\beta \eta_{K,1}}{1 + \beta \eta_{K,1}}.$$

As in a standard model without ecosystem services, optimal savings in physical capital increase with patience β and with the elasticity $\eta_{K,1}$ of date-1 output to capital K_1 (note that here the intertemporal elasticity of substitution is 1).

[21] It is straightforward to extend the results to a more general loss function $\mathcal{L}(s_{g,0}, u)$, so that $s_{g,1}(u) = s_{g,0} - \mathcal{L}(s_{g,0}, u)$, which could incorporate additional non-linearities and state-dependencies through the cross-derivative ${}^{\partial^2 \mathcal{L}}/_{\partial u \partial s_{g,0}}$. A negative cross-derivative means that land use becomes more destructive for the remaining biodiversity as species losses accumulate over time, whereas a positive cross-derivative would capture a situation where remaining species are more robust to land use, for instance through selection effects where the most fragile species disappear first. $\mathcal{L}(s_{g,0}, u)$ could also capture forces that may increase, rather than decrease, biodiversity. Since the time scales for increases in biodiversity tend to be significantly longer than the fast pace at which biodiversity is destroyed due to human activity, we do not account for them here.

The most intuitive way to write the optimality condition with respect to land use is also to express it as an optimal land conservation rate $1-u^*$, which is the counterpart of the savings rate ρ^* but for *natural* capital. Effectively, the country can invest in two assets to shift consumption between periods: physical capital and natural capital. The planning problem thus combines a standard consumption-saving tradeoff with a portfolio choice problem between the two assets. At the optimum, equalizing the marginal returns on these two forms of capital implies that optimal conservation must satisfy

$$1-u^* = \Lambda \frac{d\log E_1}{d\log(1-u)}, \tag{22}$$

where

$$\Lambda = \frac{\beta\eta_{E,1}}{\eta_{L,0}\left(1+\beta\eta_{K,1}\right)} \tag{23}$$

can be viewed as the marginal rate of substitution between future ecosystem services and current land use. A higher elasticity of date-1 output to ecosystem services, $\eta_{E,1}$, increases Λ and thus the optimal conservation to account for the higher future output costs of nature loss relative to the immediate output benefits. Of course, except in the Cobb-Douglas case ($\xi \to 1$), Λ itself is determined in equilibrium, and Appendix C.4 fully characterizes it. Besides Λ, the key object in the general optimality condition (22) is the elasticity of ecosystem services to land conservation (which is also an equilibrium object, thus depending on u^*, as we discuss below). Using equation (21), we can solve equation (22) further to express the optimal conservation $1-u^*$ as:

$$1-u^* = \Lambda \times \Big\{ \underbrace{1}_{\substack{\text{Max. abundance}\\ \text{per species}}} + \underbrace{\delta(1-u^*)\mathcal{F}(\boldsymbol{s}_1)}_{\text{Biodiversity}} \Big\}, \tag{24}$$

which leads to the following result:

Proposition 3. *The optimal conservation of natural capital satisfies*

$$1-u^* = \min\left\{1, \frac{\Lambda}{1-\Lambda\delta\mathcal{F}(\boldsymbol{s}_1)}\right\}, \tag{25}$$

where $\boldsymbol{s}_1 = \boldsymbol{s}_0 - \delta u^* \mathbf{1}$ *and* $\mathbf{1}$ *is the unit vector in* $\mathbb{R}^G$.

Comparative statics: *The optimal conservation* $1-u^*$ *decreases with initial biodiversity* $\boldsymbol{s}_0$ *and the substitutability between functions* σ*, and increases with patience* β*, the weight on ecosystem services in production* a_E*, and the magnitude of species loss induced by land use* δ*. It is independent of the initial capital stock* K_0 *if* $\xi = 1$*, and increases with* K_0 *if* $\xi < 1$.

Discussion. Equation (25) provides a characterization of the optimal conservation of nature $1-u^*$. When land use only affects abundance, with no impact on species loss (i.e., $\delta = 0$), our framework corresponds to a standard exhaustible resource problem (see Hotelling, 1931; Dasgupta and Heal, 1974).

In the presence of biodiversity loss from land use, $\delta > 0$, the optimal conservation problem is richer, but the optimal solution can be mapped to the notion of fragility. Effectively, biodiversity loss implies a

marginal cost of depleting natural capital that increases sharply with past species loss and thus past land use. The effect depends endogenously on how functions interact to produce ecosystem services (through the parameter σ), and on the within-function gains from biodiversity, captured by the parameter ϕ_g.

Equation (25) is not a closed-form solution because u^* also affects the right-hand side $\mathcal{F}(\boldsymbol{s}_1) = \mathcal{F}(\boldsymbol{s}_0 - \delta u^* \mathbf{1})$, but it is sufficient to derive the main comparative statics.[22] As shown in Section 2.2, a lower substitutability σ between functions increases fragility and therefore optimal conservation. The optimal conservation of natural capital decreases with initial biodiversity $\boldsymbol{s}_0$, as an economy starting with more biodiversity has more room to deplete its natural capital before suffering from harmful economic effects. Optimal conservation also increases with the importance of ecosystem services in production a_E and with patience β. Finally, the complementarity between physical and natural capital captured by $\xi < 1$ implies that capital-rich countries, with a higher K_0, should invest more in biodiversity preservation, by reducing their land use. The reason is that capital-rich countries are able to save more out of their current output, and thus reach a higher future physical capital K_1. As a result, in the future (at $t = 1$) natural capital will be the relatively scarcer factor of production in those richer countries, which implies that conservation of natural capital has a higher return and should optimally be higher.

Extension 1: Targeted Land Use. A key challenge specific to biodiversity relative to the extraction of other exhaustible resources is that the richness of ecosystem services and their interactions makes it difficult to fine-tune land use to preserve the most critical ecosystem functions. However, in Appendix C.6 we consider an alternative set-up in which the social planner can target conservation activities to specific functional groups. Intuitively, the economic gains from corrective policies can be maximized by targeting conservation efforts towards species loss in those functions with little remaining redundancy, as well as those functions whose current output is binding for overall ecosystem productivity. More specifically, conservation efforts aimed at minimizing the economic costs of biodiversity loss should aim to equalize the MRS between all pairs of functions to 1.

Extension 2: Nature in the utility function. In order to highlight the tradeoffs between land use and biodiversity loss from an economic perspective, our baseline model abstracts from the broader ethical question of whether the value of nature is best approached from the anthropogenic perspective of the loss of ecosystem services that are useful to humans, or whether species existence should be given some weight per se. We also do not discuss how biodiversity loss might affect the provision of 'cultural ecosystem services' such as recreational opportunities that nature provides, which can enter households' utility functions directly without affecting output.

It is straightforward to expand our framework to incorporate such additional considerations through non-pecuniary benefits from nature conservation. In Appendix C.7, we extend the model to allow for an additional date-1 utility $\nu \log E_1$ capturing direct benefits of nature conservation above and beyond the effect of ecosystem services on economic production. Our results are identical up to a redefinition of the term Λ, which becomes $\Lambda = \frac{\beta(\eta_{E,1}+\nu)}{\eta_{L,0}(1+\beta\eta_{K,1})}$ to account for the utility benefits of conservation. Thus, $\nu > 0$ leads to a higher value of Λ and therefore higher optimal conservation.

[22] In Appendix C.5 we provide analytical solutions for optimal conservation in two tractable cases: the no-substitution limit $\sigma \to 0$; and the case when initial biodiversity is symmetric across functions.

5 Conclusion

This paper makes progress in advancing our understanding of the economic effects of biodiversity loss by developing a tractable framework, grounded in insights from ecology, that captures how species interact within and across ecosystem functions to produce the aggregate ecosystem services that enter economic production functions. The model highlights the non-linear relationship between species loss and economic activity, and generates several key implications.

First, the framework emphasizes that a lack of large economic losses from past biodiversity declines does not imply that future biodiversity losses will also have limited impacts. Instead, we show that a key consequence of past species loss has been to increase the fragility of ecosystems such that any future losses will have increasingly severe economic repercussions. Consistent with this conclusion, we found that various components of a country's biodiversity risk exposure already appear to be affecting asset prices today. Policymakers should thus consider the intertemporal trade-offs associated with biodiversity loss, even if the near-term economic impacts appear modest.

Second, the model underscores that not all species are equally important for economic activity. Conservation efforts aimed at minimizing the economic costs of further biodiversity loss should prioritize species in ecosystem functions with little remaining redundancy and those functions whose output currently constrains overall ecosystem productivity. The framework provides a way to quantify the marginal economic value of different species which can help guide policy decisions around Pigouvian taxes, conservation efforts, and the design of biodiversity offsets.

Our analysis represents only a first step in modeling and measuring aggregate biodiversity risk and the relationship with the economy, and there remain important avenues for extending our analyses. First, the model could feature a richer specification of the input-output relationships across ecosystem functions, that would allow researchers to capture asymmetries across functions in terms of their importance to overall ecosystem functioning. Second, the model could be expanded to feature multiple industries with heterogeneous exposures to different ecosystem services, which would allow a specification of different degrees of substitutability between physical capital and various ecosystem services (e.g., perhaps fertilization can be more easily substituted through physical capital than pollination). Third, the model could be expanded to better incorporate the geographic nature of ecosystems. For example, we could allow the production of ecosystem services in a location to depend on the level of biodiversity in other locations. In addition, some of the ecosystem services can be traded across locations (e.g., timber and food), and this could be explicitly studied in the model. Fourth, understanding the interactions between climate change and biodiversity loss—especially how carbon sinks, climate change, and species loss feed back into one another—also represents a promising avenue of theoretical and empirical study (see Giglio et al., 2025, for a first step).

In addition to these possible enhancements on the modeling side, it is important to mention the importance of improvements on the measurement side. The growing availability of comprehensive species-level biodiversity datasets carries a lot of promise for allowing researchers to estimate and calibrate models like the one we introduce in this paper, and derive concrete policy implications. But much more empirical work is required to help these efforts fully bring the models to the data.

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A Empirical Analysis - Further Details

In this Appendix, we provide further details on the data and data construction behind the results presented in Section 2.3 and Section 3.2 of the main paper. We also present additional results that highlight the robustness of our baseline findings to variations in the empirical specification.

A.1 Details on Data Sources and Sample Construction

Map of Life Data. To proxy species abundance in each country over time, we use the Map of Life database compiled by Jetz, McPherson and Guralnick (2012). The Map of Life aggregates 532 species range datasets, including both direct observations and expert predictions, to provide comprehensive spatial data on habitat boundaries, size, and suitability for terrestrial vertebrates. This spatial data is used to calculate area scores at the species and country levels from 2001 to 2021. Here, area is defined as the product of habitat suitability (ranging continuously from 0 to 1) and habitat size. A species' area score in a given country and year represents its habitat-suitable area as a percentage of its 2001 area, with a value of 100 corresponding to a habitat-suitable area equal to that of 2001, and a value of less than 100 corresponding to a decline in habitat-suitable area.

We additionally use this data to calculate habitat scores at the species and country levels from 2001 to 2021. The habitat score is the average of a species' area score (as defined above) and its connectivity score. Here, connectivity is defined as the average distance from any point within a suitable habitat to the nearest boundary. Similarly, a species' connectivity score in a given country and year represents its habitat connectivity as a percentage of its 2001 connectivity, with a value of 100 corresponding to a habitat connectivity equal to that of 2001, and a value of less than 100 corresponding to a decline in connectivity. We use this habitat score as an alternative measure of habitat destruction for our robustness checks in Table A.11.

TetrapodTraits. To obtain categorizations of species into functional groups, we use the TetrapodTraits resource created by Moura et al. (2024). TetrapodTraits provides taxonomic data for 33,281 tetrapod species—including order, suborder, and family. These progressively finer taxonomic ranks reflect evolutionary relationships, as well as subjective groupings based on functional and genetic similarities. Each of these criteria is associated with a higher likelihood that species within the same taxonomic group will perform similar ecosystem functions. As evolutionary relationships become closer, genetic similarity increases, which often leads to the development of similar functional traits (Webb et al., 2002; Safi et al., 2011). Thus, we use these taxonomic ranks as proxies for ecosystem functional groups.

We merge this data with the Map of Life data, and calculate unweighted average area scores across all species for different definitions of functional groups. We then calculate the unweighted across-group standard deviations (and mean) of habitat loss in each country in 2021. In Table A.2, we report summary statistics by country. For example, in Argentina we have data on 1,119 unique species belonging to 132 families, 48 suborders, and 40 orders. Across these species, the 2021 area score has a standard deviation of 8.09; the within-family average area score has a standard deviation of 5.8 across families. In Figures A.2 and A.3, we map across-family and across-order mean and standard deviation of area scores in 2021 for countries in our regression sample. In Table A.3, we additionally report the count, across-group mean, and across-group standard deviation of area scores in 2021 for countries outside our sample.

Our final measure is the across-family standard deviation of the area score in 2021. To assess the robustness of this measure, we calculate the correlation and Spearman rank correlations for all 12 combinations of the following specifications: three score types (SD, p10, and min area), two taxonomic levels (family and suborder), and two time points (2015 and 2021). These correlations presented in Tables A.4 and A.5 reveal positive relationships between our final measure and each of the alternative measures.

Environmental Performance Index. To measure the state of biodiversity in each country, we use information provided by the 2022 Environmental Performance Index (EPI) published by the Yale Center for Environmental Law & Policy (Wolf et al., 2022). The EPI provides measures of many aspects of a country's environmental performance for a large set of countries. As outlined in Section 3.2, we focus on a subset of indicators related to biodiversity and ecoysystem services. Our main measure includes two indicators in the EPI's "Biodiversity & Habitat" category measuring the physical state of nature: the "Species Habitat Index" and the "Biodiversity Habitat Index".[23] The "Species Habitat Index" (SHI) is derived from the Map of Life data discussed above, where a country's annual SHI value is the average habitat score of all species occurring in that country in that year, weighted by the proportion of their global range found within that country. This index captures the extent *"of suitable habitat within a country that remains intact for each species in that country."* Since habitat loss is one of the key drivers of extinction it captures the *"potential population losses ... and ...extinction risks of individual species."* (Wolf et al., 2022, p111). The "Biodiversity Habitat Index" (BHI) is obtained by analyzing remotely-sensed forest change and land-cover change datasets using the PREDICTS model (Newbold et al., 2015) to predict habitat conditions. This index captures the *"change in biological diversity within a country due to habitat loss, degradation, and fragmentation across that country"* (Wolf et al., 2022, p102).

In addition to these two indicators from the "Biodiversity & Habitat" category, our measure also includes the indicators in the "Ecosystem Services" and "Fisheries" category. "Ecosystem Services" encompases three indicators: Tree cover loss, which measures *"the percent reduction in a country's tree cover in forested areas ... from the reference year 2000"* and grassland and wetland loss which are defined analogously but measured relative to 1992 as the reference year (Wolf et al., 2022, p122). "Fisheries" includes three indicators: "Fish Stock Status" measures *"the percentage of a country's total catch that comes from overexploited or collapsed fish stocks"*. "Marine Trophic Index" (MTI) captures the *"ecological presssures on fish stocks"* by analyzing which trophic level or food web levels a country's fishing industry is targeting and "Fish Caught by Trawling and Dredging" measures the share of fish caught by these techniques with are particularly harmful to marine ecosystems (Wolf et al., 2022, p114).

To derive our final EPI-based measure of biodiversity destruction, we use the original relative weights for the indicators from the EPI calculation, rescaling them to sum to 100%. The scores are then reversed (calculated as 100 minus the original score) so that higher values indicate greater biodiversity degradation, while maintaining the 0 to 100 range. Table A.1 shows our EPI-based measure of biodiversity for each country in our sample, broken down by continent. The rank of each country within our sample is shown in parentheses, with better ranks corresponding to lower biodiversity destruction scores. The indicators compromising the EPI are available as of 2022, but there are also baseline versions

[23] We exclude measures of regulatory protection since they are on average negatively correlated with the physical state of biodiversity, suggesting that regulatory protection is often a response to deteriorating physical conditions.

of the indicators *"derived from applying the same methodology to data from approximately 10 years prior to current measurements"* (Wolf et al., 2022, p24). In our main empirical analysis we average over the measures at both times. Table A.8 shows that the EPI based measure of biodiversity when averaging over the baseline and 2022, and in 2022 alone are very similar. Table A.9 further shows the correlation between the baseline, 2022, and averaged measures all exceed 83%. In robustness checks, we also show that our results are similar when using only the most recent measures from 2022.

Environmental Vulnerability Index. We use the Environmental Vulnerability Index (EVI) as an alternative measure for how degraded biodiversity is in a given country. Developed in 2004 by the South Pacific Applied Geoscience Commission (SOPAC) in collaboration with the UN Environment Program and their partners (Kaly, Pratt and Mitchell, 2004), the EVI combines 50 indicators of a country's vulnerability to environmental hazards. These indicators span various categories, including natural disasters (e.g., frequency of earthquakes, tsunamis and landslides) and extreme weather events (e.g., abnormally high winds, excessive rainfall or extreme heat). While the EVI also includes indicators related to biodiversity loss—such as the number of endangered species, habitat fragmentation, and loss of vegetative cover—it does not focus exclusively on them. Higher EVI values indicate greater vulnerability.

Share of Non-Natural Capital. We use the share of non-natural capital in a country's total wealth as a proxy for how likely biodiversity services are to be binding for a country's economic output. If a country has a higher share of non-natural capital, either because it has a substantial amount of non-natural capital or because renewable natural capital is scarce, it is likely that a country's production is constrained by the limited availability of ecosystem services.

We measure a country's share of non-natural capital by the complement of the share of renewable natural resources of a country's total wealth. We obtain this measure from the Notre Dame Global Adaptation Initiative (2025) project, which collects and makes publicly available a variety of measures of country's vulnerability to climate change. Specifically, we use the indicator called "id_ecos_03" which is based on data provided by the World Bank in 2011 as part of an effort to quantify different sources of each country's wealth. The database contains the indicator for three separate years: 1995, 2000 and 2005. As shown in Table A.7, the correlation between the indicator values across these years is very high, ranging from 0.87 to 0.92. Given this consistency, we choose to use the average value across the years where the measure is available for each country, which has a correlation of over 0.96 with the individual year values. In Table A.8, we see that across countries, the share of non-natural capital is on average 89% of a country's wealth, but there is substantial variation, with non-natural capital constituting 64.5% of wealth at the 5th percentile, but up to 99.2% at the 95th percentile. In Figure A.4, we map the wealth-share of non-natural capital for each country in our sample. In Table A.6 we show the exact value for each country in our sample, broken down by continent. The rank of each country within our sample is shown in parentheses, with better ranks corresponding to a lower wealth-share of non-natural capital. A high share of non-natural capital can come from low renewable natural capital or an abundance of other capital. For example, Ecuador has the lowest share of non-natural capital in our sample, reflecting its status as one of the world's most biodiverse countries with well-preserved ecosystems. Conversely, Bahrain has the second-highest share of non-natural capital in our sample, due to its arid climate and reliance on its oil and banking sectors, which require little natural capital for production.

Correlation Across Measures. Table A.9 shows the correlation between the our different country level measures. The Biodiversity Destruction Score-Avg which we use is on average uncorrelated with the Across-Family Dispersion of Area Scores, with a correlation coefficient of 2%. This suggests that the dispersion of habitat loss is a distinct measure from total habitat losses, as outlined in Section 2.3. The Wealth-Share of Non-Natural Capital is on average negatively correlated with both the Biodiversity Destruction Score-Avg and the Across-Family Dispersion of Area Scores, with a correlation coefficient of minus 13% and minus 22% respectively. This reflects that our 3 measures capture very different concepts. Our EPI-based measure captures how much biodiversity has degraded in a given country relative to its original state. Our Map of Life-based measure captures the dispersion of this biodiversity degradation in a given country relative to its original state. The Wealth-Share of Non-Natural Capital, on the other hand, measures absolute values of non-natural capital relative to a country's total wealth. Hence, it will be low if absolute values of renewable natural resources are high, irrespective of the extent or dispersion of degradation. As outlined in Section 3.2, biodiversity is preserved the most in many countries of the Middle East, which are dominated by desert landscapes. Therefore renewable natural capital resources are not necessarily high in absolute values compared to countries with habitats naturally richer in biodiversity but possibly more depleted. In addition, the share of non-natural capital is higher for countries with substantial amounts of other capital irrespective of the state of biodiversity.

Table A.9 also shows the correlation between alternative measures for a country's state of biodiversity. The Biodiversity Destruction Score-Avg measure averages over information from 2022 and baseline data from a decade earlier. It is highly correlated with the score using only 2022 and only baseline data, with 96% and 95% correlation respectively, indicating limited changes over the decade. Using only the EPI indicators from the Biodiversity & Habitat category (excluding those from the ecosystem category) yields a correlation of 52%, suggesting that ecosystem services and fisheries capture different aspects of a country's natural resources. The Environmental Vulnerability Index is close to uncorrelated with our baseline measure. The correlation is higher at 51% when only biodiversity indicators of the EPI are included. The Across-Family Dispersion of Area Scores has an 89% correlation with the Across-Suborder Dispersion of Area Scores, suggesting that dispersion patterns remain consistent over different taxonomic levels. However, the Across-Family Dispersion of Habitat Scores only show a 62% and 63% correlation with the previous two measures, indicating that habitat connectivity does not entirely align with habitat size. These measures of dispersion remain mostly uncorrelated with the Biodiversity Destruction Score and Wealth-Share of Non-Natural Capital measures. Overall, the correlations suggests that our different measures for a country's state of biodiversity capture some common aspects but also each capture different aspects not captured by the others.

Biodiversity News. To capture news about biodiversity losses, we use the NYT Biodiversity News Series produced by Giglio et al. (2023), which is from 2000 to 2022. Giglio et al. (2023) identify articles related to biodiversity loss in the New York Times using a dictionary approach of biodiversity related terms, and classify the sentiment of these articles using Bidirectional Encoder Representations from Transformers, or BERT, a standard model from the natural language processing literature. We use the news series aggregated to the weekly level, which is shown in Figure A.1 with important events labeled. In our empirical specification, we follow Giglio et al. (2023) as well as prior work by Engle et al. (2020) and

Alekseev et al. (2022), and use residuals from an AR(1) process fitted to the news series as our measure of the unanticipated component of news.

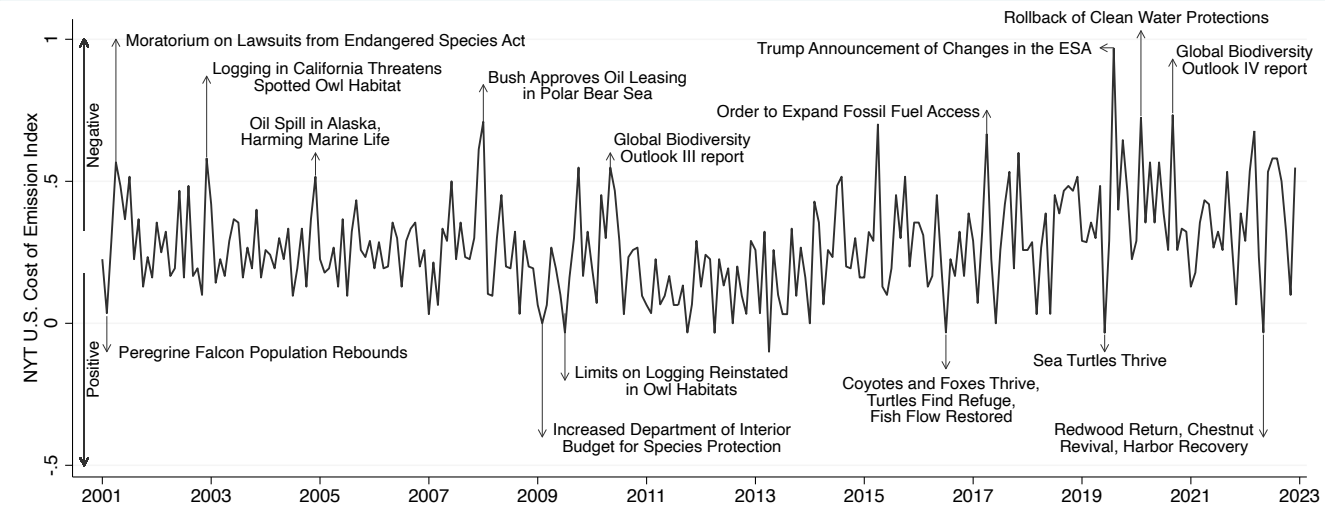
CDS Data. We obtain sovereign CDS data from Markit and include all CDS on sovereign debt contained in the database. We focus on the most liquid tenors (5, 10 and 1 years) as well as some less liquid tenors that span longer maturities (15, 20, and 30 years). We select CDS on the senior unsecured debt as it is more liquid, and keep the CDS with CR clause if available, otherwise MM, MR, and XR clauses (in this sequence); therefore, if available, we focus on CDS where the clause includes restructuring in the definition of the default event. We focus on CDS denominated in US dollars, and perform our analysis using the par spread. The par spread is the annualized cost of protection against a credit event through a CDS, and it corresponds to the way CDSs were quoted before 2009. After 2009 (in the so-called "big bang"), quoting conventions changed, with a fixed spread (100bps or 500bps) and a variable upfront payment (points upfront). Markit converts the quotes into par spread for the post-2009 period, so that it can be compared to the pre-2009 period; for the same reason, we use the par spread for the entire sample in our analysis.

A.2 Robustness Tests

Table A.11 explores robustness of our results to using alternative measures for vulnerable group habitat destruction. The first column replicates the second column of Table 1, using the across-family dispersion of area scores in 2021 as the baseline specification, while columns 2 to 8 use alternative measures. Specifically, column 2 replaces across-family dispersion with across-suborder dispersion. Column 3 adjusts the specification to use the 10th percentile of area scores across families, recoded such that lower scores (which indicate worse outcomes) correspond to higher values in the regression. Similarly, column 4 uses the minimum value of area scores across families, also recoded for consistency in interpretation. In column 5, the area scores used in the baseline are replaced with habitat scores from the Map of Life, as previously described. Column 6 has the same measure as the baseline, but using data from 2015 instead of 2021. Column 7 modifies the baseline by excluding observations from countries with less than 0.05% stewardship, defined as the proportion of a species' global habitat range within the country. Finally, column 8 address low stewardship by capping area scores at 100 for species in countries with less than 0.05% stewardship. The results are very similar regardless of the measure of habitat destruction used.

Table A.12 explores robustness of our results to using alternative measures of biodiversity destruction. Column 1 replicates the baseline specification from Table 1, using our EPI-based "Biodiversity Destruction Score" which aggregates physical indicators of biodiversity destruction, averaged between 2022 and the baseline approximately 10 years earlier. Columns 2 and 3 use the same aggregated physical indicators, but limited to 2022 and the baseline year, respectively. Column 4 replaces physical indicators with an aggregate measure of regulatory changes related to biodiversity protection. One such component of this aggregate measure is the Species Protection Index, which measures the proportion of a country's suitable habitat for a certain species that is under formal protection. Columns 5 and 6 apply the same aggregated regulatory measure, but using only 2022 and baseline data respectively. Column 7 instead uses the Environmental Vulnerability Index (EVI) developed by the South Pacific Applied Geoscience Commission (SOPAC) to assess a country's vulnerability to environmental hazards. The results are very similar irrespective of the measure used.

Figure A.1: Time Series of NYT Biodiversity News Series from 2001–2022



Note: The figure shows the monthly NYT Biodiversity News Series from 2001 to 2022 by Giglio et al. (2023), annotated with biodiversity-relevant events that have potential effects on financial markets.

Table A.1: Biodiversity Destruction Score By Country in 2021

	Biodiversity Destruction Score				
	Score	**Global Rank**		**Score**	**Global Rank**
Africa	**68.34**		Ukraine	73.51	(30)
Ghana	80.50	(4)	Russia	73.39	(31)
Nigeria	76.42	(14)	Italy	72.81	(33)
South Africa	74.59	(25)	Greece	72.39	(37)
Morocco	68.94	(50)	North Macedonia	71.53	(41)
Tunisia	68.53	(51)	Germany	71.52	(42)
Algeria	67.68	(54)	Czechia	71.51	(43)
Angola	65.61	(61)	Sweden	71.08	(44)
Egypt	57.57	(69)	Slovakia	70.06	(48)
Côte d'Ivoire	55.26	(71)	Austria	68.11	(52)
Asia	**61.77**		Croatia	67.88	(53)
Malaysia	83.19	(3)	Latvia	67.12	(57)
Indonesia	80.44	(5)	Bulgaria	66.19	(60)
Thailand	78.33	(8)	Finland	65.40	(62)
Viet Nam	75.78	(18)	Switzerland	60.31	(67)
Turkey	75.74	(19)	Norway	60.19	(68)
Korea	74.93	(24)	Malta	49.35	(74)
Cyprus	72.88	(32)	Iceland	36.68	(75)
China	71.81	(39)	**North America**	**73.44**	
Japan	70.75	(46)	Guatemala	78.85	(7)
Philippines	67.42	(56)	U.S.A.	77.15	(12)
India	66.83	(58)	Costa Rica	75.50	(20)
Sri Lanka	64.42	(64)	Panama	75.26	(21)
Israel	61.79	(66)	Trinidad and Tobago	75.23	(22)
Pakistan	56.18	(70)	El Salvador	74.35	(27)
Oman	55.08	(72)	Jamaica	72.41	(36)
Singapore	51.53	(73)	Canada	71.84	(38)
Jordan	34.43	(76)	Mexico	70.22	(47)
Bahrain	33.17	(77)	Belize	69.38	(49)
Saudi Arabia	31.04	(78)	Dominican Republic	67.58	(55)
United Arab Emirates	29.65	(79)	**Oceania**	**72.25**	
Europe	**69.96**		New Zealand	75.83	(17)
Portugal	83.72	(1)	Australia	74.18	(28)
Spain	79.32	(6)	Fiji	66.74	(59)
Belgium	77.80	(9)	**South America**	**72.16**	
Denmark	77.45	(11)	Uruguay	83.64	(2)
Poland	76.49	(13)	Argentina	77.67	(10)
Netherlands	75.92	(15)	Brazil	72.73	(34)
Ireland	75.87	(16)	Colombia	72.55	(35)
United Kingdom	75.03	(23)	Ecuador	71.71	(40)
France	74.46	(26)	Chile	71.06	(45)
Lithuania	73.67	(29)	Venezuela	65.29	(63)
			Peru	62.64	(65)

Note: The table shows the "Biodiversity Destruction Score" by country in 2021. Global rank within the sample is shown in parentheses (higher scores and higher ranks correspond to more biodiversity destruction). The score includes indicators for the change in biological diversity that has occurred in a country and for the amount of suitable habitat remaining for each species from the biodiversity and habitat category, as well as indicators on ecosystem services (loss in tree cover, grassland and wetlands) and fisheries.

Table A.2: 2021 Area Score by Taxonomic Classification and Country, In-Sample

	Species			Family			Suborder			Order		
Country	Count	Mean	SD	Count	Mean	SD	Count	Mean	SD	Count	Mean	SD
Algeria	266	102.36	4.34	83	102.35	3.51	37	102.80	3.15	31	103.13	3.17
Angola	1076	99.45	3.45	145	99.42	1.79	53	99.73	1.01	44	99.66	1.04
Argentina	1119	96.87	8.09	132	96.71	5.80	48	97.89	2.22	40	97.80	2.31
Australia	1089	98.94	5.94	120	99.26	2.96	42	99.58	2.28	35	99.82	2.34
Austria	250	99.46	2.85	70	99.69	1.79	32	99.75	1.68	28	99.86	1.75
Bahrain	29	93.50	13.86	20	94.03	13.69	12	92.38	10.72	10	93.03	11.64
Belgium	196	98.32	2.90	64	98.40	2.11	30	98.22	2.44	26	98.27	2.54
Belize	556	96.59	8.19	107	96.64	5.59	42	96.52	5.29	34	96.76	5.02
Brazil	2463	96.69	6.22	155	97.08	3.13	47	97.75	2.06	38	97.76	2.10
Bulgaria	295	99.55	1.74	78	99.55	1.19	35	99.59	1.02	29	99.61	1.04
Canada	413	98.97	3.97	86	99.09	2.24	33	98.91	2.00	28	99.02	2.02
Chile	309	98.98	4.53	75	99.15	3.30	33	98.77	4.27	28	99.45	1.58
China	1768	98.34	6.13	156	98.15	5.51	48	97.05	7.59	39	98.44	2.27
Colombia	2468	97.40	5.53	159	97.70	3.25	50	98.25	2.55	41	98.35	2.47
Costa Rica	1061	97.98	5.08	127	98.62	3.05	44	98.70	2.52	36	99.12	2.34
Croatia	292	99.40	1.24	82	99.45	0.68	36	99.44	0.55	30	99.49	0.55
Cyprus	114	99.15	2.55	50	98.81	2.25	28	98.64	2.27	22	98.98	2.08
Czech Republic	219	99.02	2.80	68	99.30	1.44	31	99.13	1.82	27	99.15	1.94
Côte d'Ivoire	717	97.64	11.54	131	97.82	6.37	48	98.35	4.24	40	98.16	4.16
Denmark	175	99.57	1.32	64	99.61	0.71	29	99.57	0.72	25	99.60	0.75
Dominican Republic	208	99.86	2.83	66	99.87	1.72	31	99.91	1.30	26	99.99	1.29
Ecuador	1935	98.10	4.27	149	98.01	3.34	50	98.08	2.82	41	98.22	2.68
Egypt	240	100.53	3.67	81	100.73	3.17	36	101.08	3.46	30	101.31	3.71
El Salvador	525	98.76	3.21	104	98.77	2.29	42	98.85	1.70	34	98.73	1.85
Fiji	34	99.84	1.97	19	100.22	1.93	11	100.68	2.32	9	101.02	2.42
Finland	179	100.39	8.99	61	100.83	4.69	28	100.55	5.23	25	100.68	5.53
France	336	99.49	1.71	93	99.68	1.25	38	99.71	1.24	32	99.52	0.76
Germany	264	99.08	1.65	76	99.18	1.06	33	99.11	1.20	29	99.13	1.24
Ghana	700	100.44	5.22	134	100.58	3.01	47	100.97	1.94	39	100.88	1.84
Greece	326	99.71	1.09	84	99.79	0.72	37	99.77	0.64	30	99.73	0.69
Guatemala	882	93.05	14.00	118	93.98	8.55	43	94.30	6.52	35	93.93	6.90
Iceland	29	100.00	0.00	15	100.00	0.00	8	100.00	0.00	8	100.00	0.00
India	1470	98.98	5.15	151	99.04	2.23	48	98.69	2.62	40	98.93	1.76
Indonesia	2218	96.16	12.21	171	97.61	11.89	56	96.82	4.96	45	97.00	5.37
Ireland	94	100.85	1.68	44	100.62	1.25	22	100.35	1.01	22	100.35	1.01
Israel	258	99.02	2.79	82	98.86	2.16	33	98.97	2.12	27	99.15	2.30
Italy	331	99.41	1.89	89	99.52	1.02	37	99.45	0.87	31	99.48	0.90
Jamaica	143	98.26	3.52	54	98.75	2.87	25	98.60	1.59	22	98.68	1.64
Japan	325	98.64	2.43	93	98.77	1.86	36	98.63	1.54	30	98.62	1.47
Jordan	241	99.19	2.11	76	99.07	1.54	30	98.95	1.31	24	99.16	1.16
Latvia	197	99.41	5.91	65	100.09	3.20	30	99.99	3.79	26	100.08	4.07
Lithuania	194	99.38	3.00	65	99.64	1.52	30	99.61	1.72	26	99.56	1.83
Macedonia	260	99.21	2.58	75	99.25	1.85	35	99.16	1.76	29	99.19	1.79
Malaysia	1080	93.00	15.96	132	96.61	14.28	46	95.32	8.65	37	96.39	8.99
Malta	23	98.87	3.55	17	98.96	3.07	13	99.31	2.75	10	99.57	2.31
Mexico	1600	97.00	7.32	146	97.65	3.70	50	97.63	3.13	41	97.49	3.32
Morocco	294	100.47	2.89	94	100.53	1.82	39	100.95	2.11	33	101.06	2.12
Netherlands	195	98.48	2.38	66	98.47	1.61	30	98.29	1.56	26	98.27	1.61
New Zealand	105	99.22	4.27	40	99.26	2.75	24	99.39	2.34	22	99.39	2.42
Nigeria	932	99.23	4.01	145	99.06	2.91	53	99.29	2.30	44	99.38	2.22
Norway	177	100.59	4.52	62	100.79	3.38	29	100.46	4.15	26	100.62	4.34
Oman	150	99.58	2.45	60	100.02	1.40	26	99.94	1.09	22	100.08	0.74

Table A.2: 2021 Area Score by Taxonomic Classification and Country, In-Sample

	Species			Family			Suborder			Order		
Country	Count	Mean	SD	Count	Mean	SD	Count	Mean	SD	Count	Mean	SD
Pakistan	576	99.85	3.54	115	100.06	1.94	39	99.78	1.68	32	99.95	1.49
Panama	1155	97.47	5.22	134	97.94	2.97	43	97.83	2.57	36	98.09	2.51
Peru	2054	97.90	4.91	155	98.53	2.06	50	99.01	1.27	41	99.02	1.32
Philippines	806	97.21	7.32	113	97.89	3.73	40	98.02	2.28	32	98.25	2.13
Poland	240	99.41	1.74	69	99.51	0.90	30	99.39	1.12	26	99.33	1.18
Portugal	262	99.33	2.29	86	99.60	2.53	38	99.42	2.16	31	99.67	2.23
Russia	643	99.75	2.90	110	99.77	1.51	39	100.00	1.71	32	99.79	1.18
Saudi Arabia	239	100.55	3.62	80	100.37	1.92	32	100.48	1.93	26	100.65	2.09
Singapore	391	84.01	19.05	98	83.69	15.29	38	83.50	13.05	31	82.13	13.12
Slovakia	229	99.37	2.31	69	99.38	1.05	31	99.21	1.12	26	99.19	1.21
South Africa	952	99.31	3.00	145	99.34	1.96	53	99.66	1.61	43	99.49	0.77
South Korea	189	99.05	3.27	74	99.21	2.95	31	99.08	2.50	26	98.88	2.59
Spain	353	99.33	1.97	97	99.35	1.26	42	99.22	1.35	35	99.38	1.28
Sri Lanka	399	99.28	2.93	104	99.59	1.61	42	99.35	1.37	35	99.54	1.30
Sweden	194	100.07	8.28	65	100.84	5.39	29	100.78	5.85	25	101.07	6.26
Switzerland	230	98.59	1.77	64	98.79	1.31	30	98.75	0.99	26	98.81	1.02
Thailand	1258	96.67	8.69	140	97.37	5.05	47	97.04	3.42	39	97.53	3.29
Trinidad and Tobago	435	98.36	2.91	103	98.08	2.82	41	98.32	1.31	33	98.28	1.37
Tunisia	230	102.48	5.30	80	102.35	3.89	35	102.33	3.43	29	102.40	3.52
Turkey	453	99.13	3.01	97	99.25	1.04	39	99.20	0.97	32	99.16	1.03
Ukraine	299	99.27	2.24	79	99.28	1.33	36	99.19	1.45	30	99.14	1.57
United Arab Emirates	104	100.10	1.89	52	100.06	1.54	22	100.16	1.04	18	100.27	1.11
United Kingdom	170	99.32	1.61	59	99.40	0.85	29	99.29	0.82	26	99.29	0.85
United States	1045	98.05	7.39	131	98.54	5.05	45	99.07	2.22	37	99.12	2.35
Uruguay	370	99.65	3.93	90	99.91	2.64	39	100.14	1.84	32	100.18	1.88
Venezuela	1681	98.90	2.83	143	99.08	1.57	45	99.35	1.10	37	99.39	1.13
Vietnam	1140	96.90	6.90	137	97.59	5.09	47	95.48	5.34	38	96.22	5.22

Note: The table shows the count, as well as the mean and standard deviation of area scores across species, families, suborders and orders in 2021 for each country in our final regression sample.

Table A.3: 2021 Area Score by Taxonomic Classification and Country, Out-of-Sample

	Species			Family			Suborder			Order		
Country	Count	Mean	SD	Count	Mean	SD	Count	Mean	SD	Count	Mean	SD
Afghanistan	368	100.13	3.21	91	100.18	1.38	32	100.23	1.18	26	100.31	0.98
Akrotiri and Dhekelia	48	98.88	2.46	30	98.62	2.13	18	98.52	1.80	13	98.62	2.05
Albania	264	99.08	2.31	77	99.19	1.58	34	99.19	1.61	28	99.28	1.67
Andorra	99	99.51	0.55	44	99.49	0.51	20	99.54	0.59	16	99.56	0.66
Anguilla	21	100.91	1.22	15	101.02	1.17	10	101.19	1.05	7	101.10	1.06
Antigua and Barbuda	35	97.80	3.76	23	97.90	3.22	14	97.89	3.25	13	97.79	3.32
Armenia	277	99.24	1.29	77	99.19	1.00	35	99.12	1.02	29	99.18	1.02
Aruba	26	95.95	12.16	19	94.40	12.83	14	95.14	13.81	12	94.90	14.91
Azerbaijan	313	99.85	1.30	80	99.78	0.75	36	99.75	0.76	29	99.81	0.76
Bahamas	114	101.33	1.99	47	101.37	1.72	26	101.49	1.99	23	101.36	2.04
Bangladesh	586	98.95	6.21	116	99.05	2.57	40	98.65	2.62	33	98.73	2.51
Barbados	32	99.08	5.56	23	98.91	5.27	15	99.29	6.24	10	99.74	4.98
Belarus	218	99.48	2.00	67	99.63	1.27	30	99.68	1.42	26	99.61	1.38
Benin	587	100.37	5.11	121	100.41	5.89	47	101.14	2.71	39	101.12	2.55
Bhutan	612	99.89	1.70	116	100.00	1.20	39	99.92	0.79	31	99.85	0.74
Bolivia	1690	98.30	5.04	143	98.35	3.44	47	98.86	2.99	38	99.00	3.22

Table A.3: 2021 Area Score by Taxonomic Classification and Country, Out-of-Sample

	Species			Family			Suborder			Order		
Country	Count	Mean	SD	Count	Mean	SD	Count	Mean	SD	Count	Mean	SD
Bonaire, Sint Eustatius & Saba	50	100.13	3.15	32	99.96	3.04	17	99.98	2.02	13	99.92	2.08
Bosnia and Herzegovina	274	99.04	2.33	79	98.93	3.18	35	98.93	3.10	29	99.44	0.71
Botswana	642	100.59	2.25	131	100.47	1.17	49	100.62	0.92	40	100.69	0.91
British Virgin Islands	40	97.26	6.97	26	97.90	6.15	14	97.63	5.07	12	98.13	4.52
Brunei	615	98.48	2.87	108	98.80	1.27	40	98.50	0.78	32	98.47	0.80
Burkina Faso	472	100.44	4.27	117	100.55	2.85	44	100.39	2.59	37	100.02	2.15
Burundi	713	100.03	2.15	127	100.06	1.43	47	99.97	1.30	39	100.15	0.98
Cambodia	713	95.01	12.12	122	96.35	8.75	44	94.58	7.89	36	95.30	7.79
Cameroon	1039	98.51	4.53	144	98.37	4.57	50	98.62	2.31	41	98.94	1.83
Cape Verde	15	99.97	0.93	10	99.99	0.72	7	100.02	0.80	7	100.02	0.80
Cayman Islands	48	99.60	5.00	24	99.61	3.56	14	100.25	4.56	11	99.62	3.12
Central African Republic	815	99.48	2.32	135	99.60	1.31	50	99.61	1.01	41	99.70	0.94
Chad	539	99.93	3.20	119	100.03	2.12	45	100.12	1.59	39	100.13	1.66
Comoros	56	99.20	3.18	28	99.34	1.94	13	99.44	2.24	10	99.23	2.48
Cuba	215	99.08	3.89	62	99.68	1.62	31	99.52	1.03	25	99.49	1.09
Curaçao	39	97.71	10.21	28	97.24	10.81	16	97.98	8.99	13	97.88	9.94
Dem. Rep. of the Congo	1374	98.89	7.25	148	99.18	5.75	55	99.65	2.81	46	99.97	2.86
Djibouti	226	101.11	4.87	90	101.19	3.68	37	101.49	2.29	32	101.59	2.37
Dominica	61	96.00	14.08	35	96.52	11.05	16	97.48	5.72	12	96.72	6.47
Equatorial Guinea	535	101.37	22.10	119	103.40	25.35	46	104.16	16.49	37	105.12	18.12
Eritrea	452	100.42	1.51	118	100.38	1.17	46	100.49	0.96	40	100.56	0.90
Estonia	191	99.92	5.99	64	100.43	3.79	30	100.42	4.21	26	100.62	4.49
Ethiopia	875	100.32	2.50	137	100.36	1.18	47	100.38	0.82	39	100.35	0.84
Falkland Islands	32	99.36	0.57	24	99.46	0.58	13	99.47	0.53	12	99.43	0.54
French Guiana	829	99.96	3.65	120	100.01	2.08	43	100.09	1.20	35	100.02	0.88
French Polynesia	22	100.00	0.00	10	100.00	0.00	7	100.00	0.00	7	100.00	0.00
Gabon	630	100.35	4.38	128	100.35	1.77	47	100.38	1.54	38	100.49	1.68
Gambia	424	100.46	3.41	113	100.66	2.46	43	100.98	2.21	36	101.12	2.10
Georgia	297	99.52	1.00	80	99.39	0.85	38	99.27	0.89	31	99.35	0.76
Greenland	28	100.00	0.00	15	100.00	0.00	7	100.00	0.00	7	100.00	0.00
Grenada	56	99.07	3.73	32	98.78	4.25	16	99.59	1.54	13	99.50	1.71
Guadeloupe	64	98.08	11.83	36	98.46	9.56	18	97.34	4.85	14	97.64	5.26
Guernsey	20	97.49	3.81	17	97.37	3.63	12	97.15	4.03	12	97.15	4.03
Guinea	723	99.04	8.60	134	98.72	6.36	48	99.25	3.04	40	99.16	3.21
Guinea-Bissau	441	100.52	7.10	112	100.34	4.83	44	99.92	3.14	37	100.20	3.08
Guyana	1019	99.72	2.16	127	99.86	1.03	44	99.97	0.81	36	100.02	0.86
Haiti	204	98.25	2.40	65	98.38	1.85	31	98.20	1.76	26	98.33	1.86
Honduras	924	92.65	14.56	123	93.59	9.50	44	94.58	5.91	36	94.35	6.01
Hong Kong	279	97.82	4.34	85	97.38	3.86	36	97.98	3.56	28	97.63	3.55
Hungary	242	99.58	2.49	69	99.57	1.30	33	99.51	1.54	28	99.55	1.64
Iran	506	100.91	4.01	100	101.05	2.10	37	101.25	1.97	31	101.53	1.96
Iraq	301	100.25	1.95	82	100.32	1.26	34	100.23	1.02	28	100.37	1.03
Isle of Man	27	99.52	1.10	23	99.53	1.16	13	99.72	1.35	13	99.72	1.35
Jersey	36	99.00	2.95	23	98.56	2.01	14	98.49	1.97	14	98.49	1.97
Kazakhstan	397	101.63	3.37	91	101.66	3.65	36	101.50	1.76	29	101.87	1.53
Kenya	1181	100.22	2.36	153	100.31	1.62	53	100.33	0.90	44	100.24	0.91
Kosovo	244	99.31	1.78	72	99.32	1.44	34	99.14	1.62	28	99.17	1.60
Kuwait	71	100.64	4.98	37	100.76	5.53	19	101.49	7.20	14	102.26	8.32
Kyrgyzstan	237	100.03	1.52	74	100.00	1.11	34	99.77	0.80	29	99.85	0.75
Laos	976	95.85	12.53	126	97.52	8.49	44	94.91	8.40	35	96.69	6.11
Lebanon	212	99.48	1.83	78	99.31	1.45	32	99.34	1.49	26	99.40	1.61
Lesotho	370	99.50	1.53	109	99.54	1.03	44	99.46	1.16	35	99.70	0.83

Table A.3: 2021 Area Score by Taxonomic Classification and Country, Out-of-Sample

	Species			Family			Suborder			Order		
Country	Count	Mean	SD	Count	Mean	SD	Count	Mean	SD	Count	Mean	SD
Liberia	544	99.23	22.52	121	102.29	45.27	45	98.61	3.26	37	98.59	3.47
Libya	157	99.70	1.01	63	99.74	0.59	29	99.80	0.45	24	99.85	0.40
Liechtenstein	73	96.59	4.89	36	95.98	3.78	19	96.39	3.33	16	96.46	3.42
Luxembourg	156	98.77	1.82	57	98.74	1.21	29	98.74	1.10	25	98.77	1.14
Madagascar	464	91.32	16.02	78	95.57	9.48	35	93.76	11.08	30	93.74	11.87
Malawi	717	100.72	3.22	132	100.72	1.79	48	100.88	1.75	39	101.07	1.42
Mali	538	100.67	4.30	120	100.90	4.80	46	101.08	2.18	39	100.94	1.91
Martinique	75	99.27	2.38	43	99.31	2.48	22	99.48	2.81	17	99.71	3.17
Mauritania	374	99.82	2.65	110	99.94	1.58	45	99.87	1.55	39	99.98	1.50
Mauritius	17	96.86	6.56	14	96.78	6.38	8	97.72	6.43	7	98.48	4.84
Mayotte	31	99.36	4.85	20	99.88	1.81	12	99.47	2.16	9	99.30	2.49
Micronesia	26	99.98	0.05	14	99.97	0.06	9	99.97	0.07	8	99.96	0.07
Moldova	226	99.31	2.88	67	99.35	2.55	31	99.12	1.39	27	98.97	1.33
Mongolia	289	101.53	4.42	68	101.12	3.03	30	101.53	1.93	27	101.68	1.97
Montenegro	251	98.33	2.63	74	98.55	1.75	35	98.60	1.61	29	98.74	1.46
Montserrat	25	99.47	3.91	17	99.16	4.63	10	100.68	2.32	7	100.78	2.72
Mozambique	831	99.74	3.53	143	99.74	1.91	51	99.88	1.73	42	99.94	1.79
Myanmar	1298	97.34	7.86	143	97.87	4.46	48	97.41	4.29	40	97.83	4.19
Namibia	716	101.21	3.40	135	101.20	1.56	51	101.21	1.28	42	101.18	1.27
Nepal	713	99.98	1.20	119	99.90	0.63	41	99.83	0.84	33	99.86	0.60
New Caledonia	83	100.28	1.97	28	99.79	2.12	15	99.30	2.59	14	99.22	2.66
Nicaragua	851	90.94	18.76	124	91.98	11.77	44	93.08	8.75	36	93.63	8.14
Niger	445	99.21	2.34	112	99.20	1.55	43	99.14	0.88	37	99.14	0.91
North Korea	242	99.52	2.47	79	99.52	2.19	33	99.44	1.95	29	99.50	2.01
Northern Cyprus	103	98.52	2.84	50	98.46	2.44	27	98.32	2.31	21	98.56	2.47
Northern Mariana Islands	16	100.00	0.00	13	100.00	0.00	8	100.00	0.00	6	100.00	0.00
Palau	32	98.95	4.34	21	99.02	4.92	12	100.05	5.88	9	100.75	6.62
Palestina	206	97.75	4.13	78	97.70	3.20	33	97.39	3.90	27	97.62	4.09
Papua New Guinea	839	99.04	3.21	99	99.37	1.60	37	99.08	1.34	30	98.99	1.43
Paraguay	818	94.69	13.74	116	94.11	9.40	44	95.35	5.53	36	95.30	6.00
Puerto Rico	144	96.46	9.98	56	97.34	5.40	29	96.96	4.90	23	96.88	5.48
Qatar	46	100.82	5.40	28	101.54	6.26	17	102.76	7.70	13	103.74	8.62
Republic of Congo	747	100.17	7.24	131	100.28	3.74	47	100.57	3.14	38	100.44	2.78
Reunion	17	98.97	7.50	13	98.88	6.58	7	97.88	6.00	7	97.88	6.00
Romania	288	99.23	1.43	79	99.18	1.04	35	99.19	1.03	30	99.14	1.06
Rwanda	762	100.75	3.37	124	101.04	2.43	46	100.80	2.07	38	101.07	1.77
Saint Kitts and Nevis	40	98.89	2.30	22	99.14	2.70	12	99.22	2.94	9	99.43	3.33
Saint Lucia	49	99.66	0.98	29	99.61	0.93	13	99.61	0.42	9	99.64	0.32
Saint-Barthelèmy	19	97.19	3.10	13	96.66	2.48	9	96.66	1.86	6	97.03	1.56
Saint-Martin	23	101.30	7.55	16	100.53	6.57	11	99.74	5.29	7	101.04	5.72
Samoa	16	100.00	0.00	13	100.00	0.00	7	100.00	0.00	7	100.00	0.00
San Marino	45	99.38	3.33	26	99.25	2.66	14	98.57	3.10	10	98.93	2.81
Senegal	534	100.12	3.57	121	100.20	1.77	46	100.24	1.71	39	100.17	1.80
Serbia	272	99.45	1.56	74	99.45	0.99	33	99.42	0.98	28	99.42	1.02
Seychelles	31	100.34	0.52	19	100.28	0.43	12	100.33	0.51	10	100.36	0.55
Sierra Leone	587	101.79	28.23	124	101.50	18.25	46	99.79	5.53	38	99.81	6.03
Sint Maarten	23	98.02	11.69	16	96.74	10.28	11	95.30	7.96	7	97.42	7.79
Slovenia	260	99.59	2.02	74	99.68	1.57	34	99.60	1.49	29	99.45	1.12
Solomon Islands	172	98.07	4.76	50	98.71	2.55	25	98.70	2.32	20	98.50	2.50
Somalia	633	100.10	2.42	133	100.23	2.15	47	100.24	1.37	40	100.27	1.47
South Sudan	893	101.13	3.53	138	101.18	1.99	49	101.04	1.55	40	101.16	1.07
St. Vincent & the Grenadines	50	99.74	0.44	30	99.82	0.36	15	99.79	0.24	11	99.75	0.24

Table A.3: 2021 Area Score by Taxonomic Classification and Country, Out-of-Sample

	Species			Family			Suborder			Order		
Country	Count	Mean	SD	Count	Mean	SD	Count	Mean	SD	Count	Mean	SD
Sudan	598	100.52	3.05	124	100.52	2.01	45	100.42	1.34	39	100.56	1.17
Suriname	855	99.79	2.88	123	99.63	2.32	44	99.63	1.71	36	99.57	1.83
Svalbard and Jan Mayen	15	100.00	0.00	8	100.00	0.00	4	100.00	0.00	4	100.00	0.00
Swaziland	611	99.12	3.60	130	98.81	2.40	47	98.50	2.25	37	98.76	2.25
Syria	286	99.76	1.70	88	99.67	1.42	36	99.57	1.31	30	99.59	1.42
São Tomé and Príncipe	50	99.82	1.43	33	99.95	0.32	16	99.92	0.22	14	99.91	0.22
Taiwan	378	97.89	2.55	97	97.79	2.19	34	97.67	1.63	28	97.62	1.62
Tajikistan	240	99.86	1.68	73	99.86	0.99	31	99.76	0.92	26	99.70	0.87
Tanzania	1228	100.22	4.60	150	100.02	1.39	53	100.16	1.11	44	100.03	0.65
Timor-Leste	174	99.80	1.75	68	99.94	0.84	31	99.87	0.79	27	99.86	0.82
Togo	609	100.16	6.05	122	100.36	3.92	45	100.98	2.83	37	100.91	2.91
Turkmenistan	255	100.82	2.89	74	100.80	1.80	32	100.71	1.25	27	100.83	1.27
Turks and Caicos Islands	52	99.43	1.09	29	99.68	1.08	17	99.61	0.63	13	99.61	0.42
Uganda	1122	99.87	3.51	141	99.75	2.24	50	99.95	1.28	42	100.09	1.10
Uzbekistan	260	98.80	6.21	78	98.83	3.63	33	99.27	2.14	28	99.28	2.31
Vanuatu	53	103.36	12.70	24	101.12	14.53	15	98.29	16.99	14	98.10	17.61
Virgin Islands, U.S.	58	96.93	5.17	33	96.94	4.95	23	96.84	4.52	19	97.06	3.70
Western Sahara	78	100.00	0.03	35	99.99	0.02	19	99.99	0.02	14	100.00	0.01
Yemen	236	99.43	5.02	76	99.69	2.15	30	99.71	1.22	25	99.80	1.09
Zambia	829	99.79	2.12	139	99.66	1.64	50	99.86	1.18	41	100.05	0.62
Zimbabwe	739	99.84	1.92	138	99.88	1.00	50	99.99	0.75	41	100.04	0.75
Åland	55	101.00	6.53	31	101.21	4.33	17	101.55	5.58	15	101.68	5.94

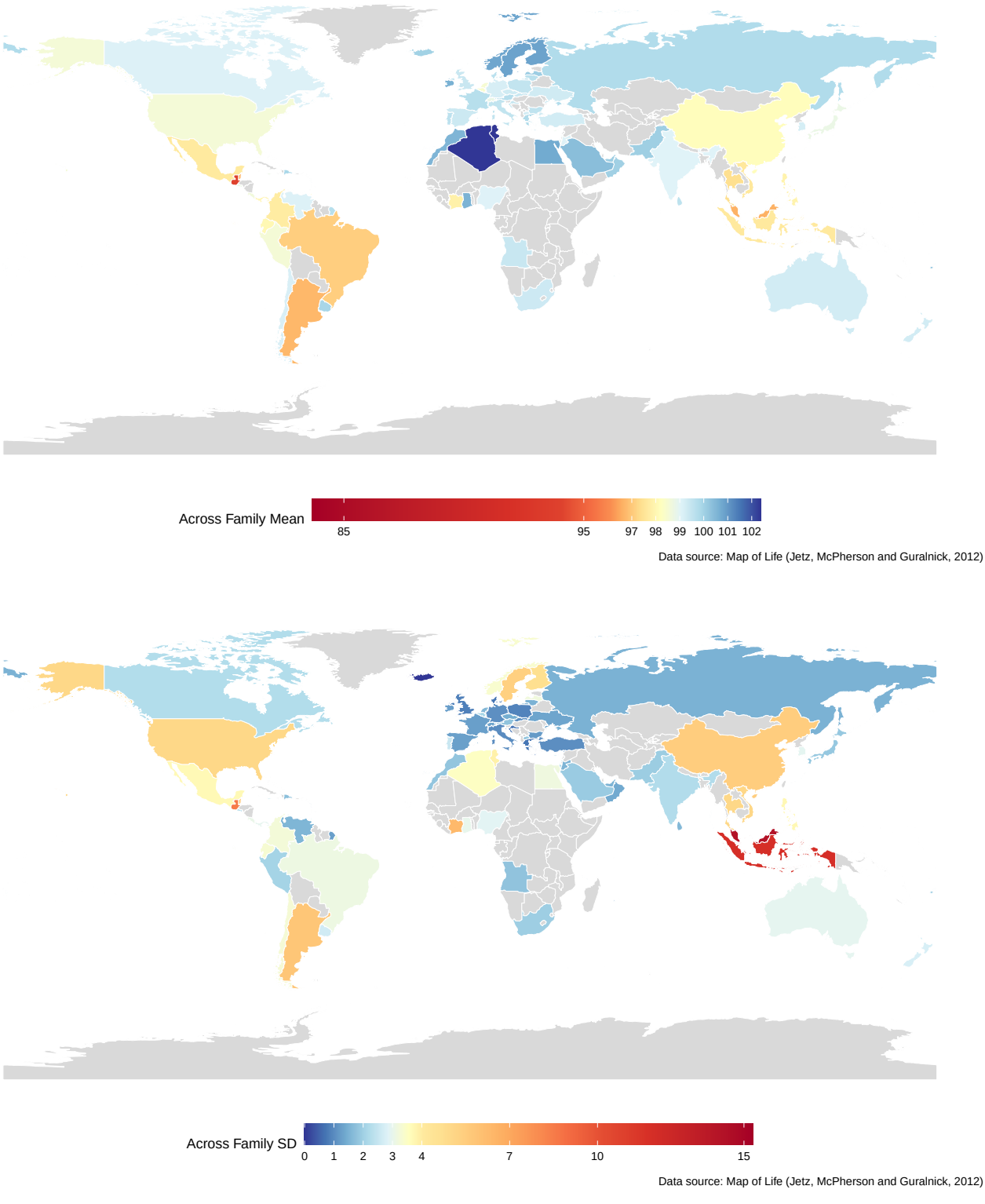
Note: The table shows the group count, as well as the mean and standard deviation of area scores across species, families, suborders and orders in 2021 for each country excluded from the final regression sample.

Table A.4: Correlation between Measures of Imbalance in Habitat Destruction

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)
(1) Across-Family SD in 2021	1.00											
(2) Across-Family p10 in 2021	0.55	1.00										
(3) Across-Family Min in 2021	0.53	0.65	1.00									
(4) Across-Family SD in 2015	0.91	0.60	0.50	1.00								
(5) Across-Family p10 in 2015	0.51	0.95	0.54	0.64	1.00							
(6) Across-Family Min in 2015	0.45	0.55	0.86	0.56	0.53	1.00						
(7) Across-Suborder SD in 2021	0.70	0.71	0.58	0.78	0.68	0.51	1.00					
(8) Across-Suborder p10 in 2021	0.55	0.87	0.61	0.65	0.87	0.57	0.80	1.00				
(9) Across-Suborder Min in 2021	0.51	0.73	0.79	0.55	0.68	0.68	0.74	0.79	1.00			
(10) Across-Suborder SD in 2015	0.61	0.62	0.46	0.81	0.68	0.55	0.92	0.79	0.66	1.00		
(11) Across-Suborder p10 in 2015	0.48	0.76	0.48	0.66	0.84	0.52	0.74	0.95	0.69	0.81	1.00	
(12) Across-Suborder Min in 2015	0.43	0.62	0.65	0.58	0.65	0.77	0.67	0.74	0.87	0.75	0.73	1.00

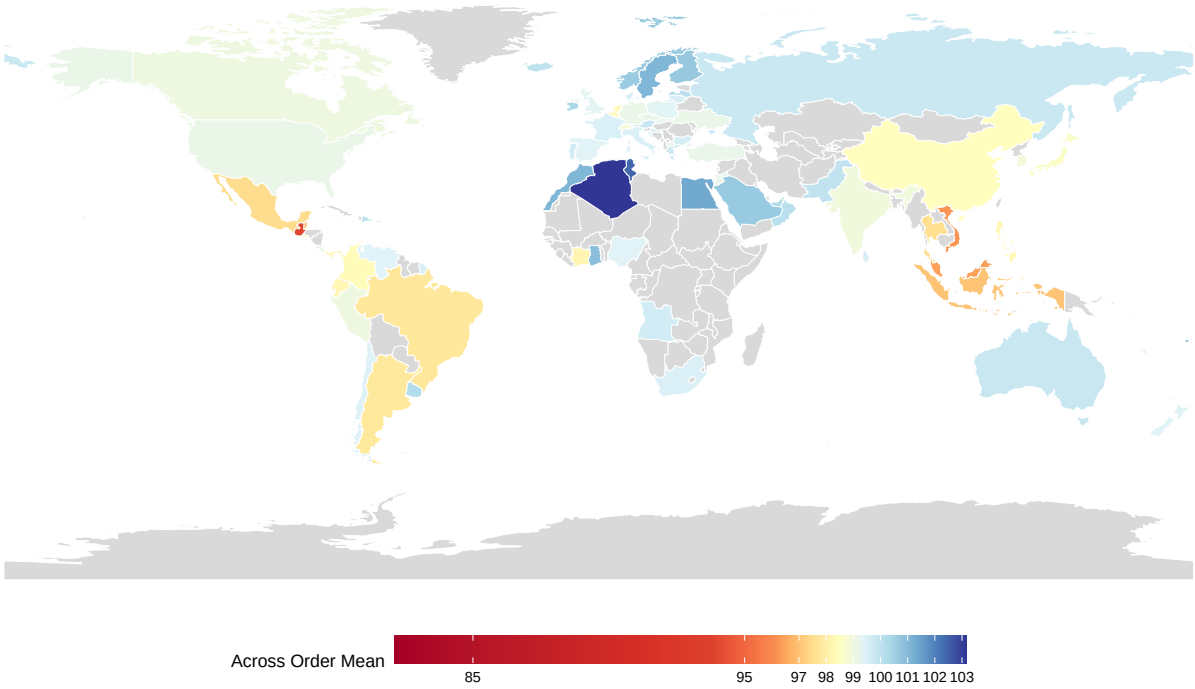
Note: The table presents correlations for all combinations of three score types—SD, p10, and min area (with p10 and min reversed)—across two taxonomic levels (family and suborder) and two years (2015 and 2021). This yields a total of 12 correlation values, between different measures of imbalance in habitat destruction aggregated from the Map of Life data (Jetz, McPherson and Guralnick, 2012).

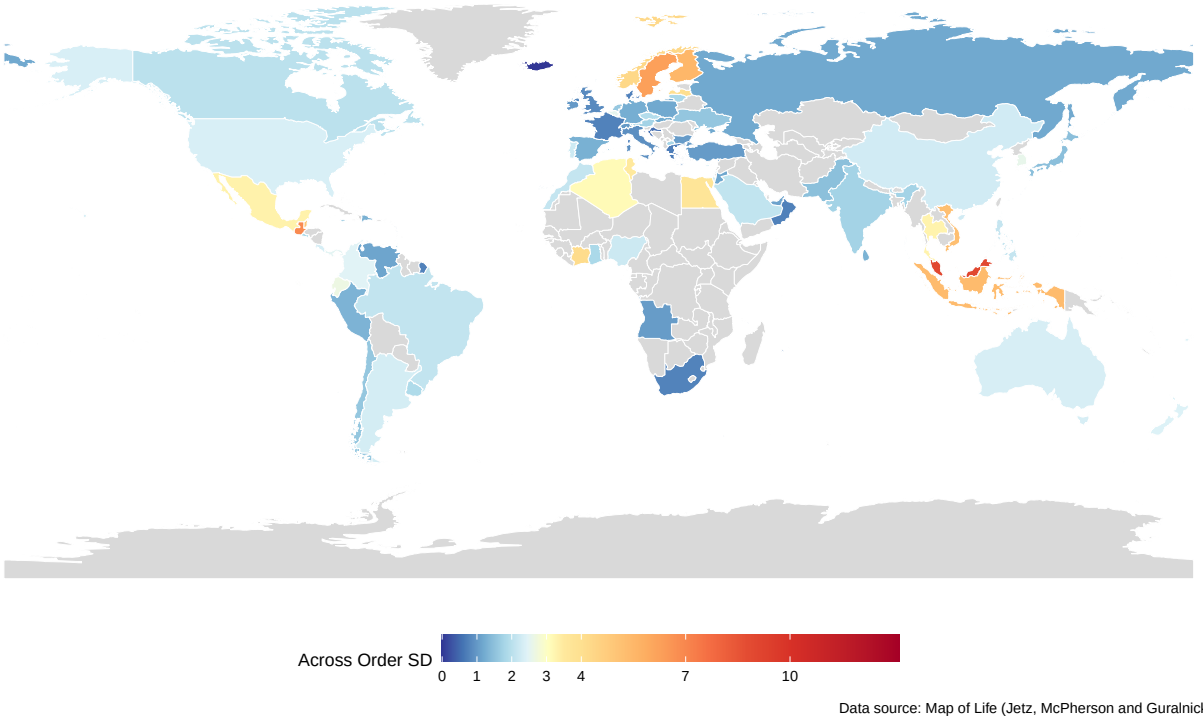
Figure A.2: Across Family Mean and Standard Deviation by Country



Note: This map shows the across-family mean and standard deviation of area scores in 2021 for each country in our final regression sample.

Figure A.3: Across Order Mean and Standard Deviation by Country





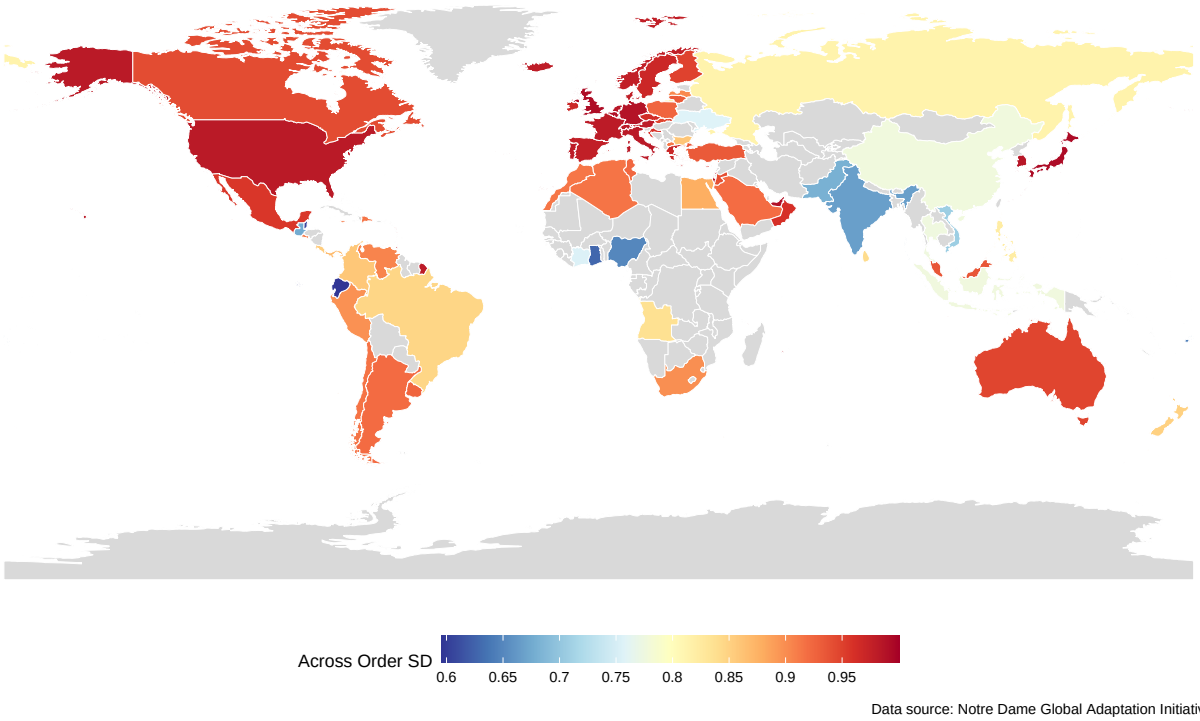
Note: This map shows the across-order mean and standard deviation of area scores in 2021 for each country in our final regression sample.

Table A.5: Spearman Rank Correlation between Measures of Imbalance in Habitat Destruction

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)
(1) Across-Family SD in 2021	1.00											
(2) Across-Family p10 in 2021	0.74	1.00										
(3) Across-Family Min in 2021	0.78	0.71	1.00									
(4) Across-Family SD in 2015	0.90	0.71	0.68	1.00								
(5) Across-Family p10 in 2015	0.68	0.93	0.63	0.74	1.00							
(6) Across-Family Min in 2015	0.73	0.68	0.89	0.79	0.68	1.00						
(7) Across-Suborder SD in 2021	0.94	0.74	0.69	0.86	0.70	0.65	1.00					
(8) Across-Suborder p10 in 2021	0.69	0.96	0.65	0.67	0.89	0.63	0.72	1.00				
(9) Across-Suborder Min in 2021	0.73	0.77	0.86	0.66	0.72	0.77	0.76	0.77	1.00			
(10) Across-Suborder SD in 2015	0.82	0.68	0.58	0.94	0.73	0.69	0.89	0.68	0.65	1.00		
(11) Across-Suborder p10 in 2015	0.64	0.89	0.59	0.69	0.96	0.65	0.68	0.92	0.71	0.71	1.00	
(12) Across-Suborder Min in 2015	0.69	0.75	0.76	0.77	0.79	0.85	0.71	0.75	0.89	0.77	0.79	1.00

Note: The table presents Spearman rank correlations for all combinations of three score types—SD, p10, and min area (with p10 and min reversed)—across two taxonomic levels (family and suborder) and two years (2015 and 2021). This yields a total of 12 correlation values, between different measures of imbalance in habitat destruction aggregated from the Map of Life data (Jetz, McPherson and Guralnick, 2012).

Figure A.4: Map of Wealth-Share of Non-Natural Capital by Country



Note: This map shows the wealth-share of non-natural capital for each country in our final regression sample.

Table A.6: Wealth-Share of Non-Natural Capital By Country

	Wealth-Share of Non-Natural Capital				
	Share	**Global Rank**		**Share**	**Global Rank**
Africa	**0.822**		Iceland	0.980	(18)
Tunisia	0.924	(41)	Denmark	0.979	(19)
Algeria	0.915	(45)	Norway	0.977	(21)
Morocco	0.914	(48)	Spain	0.977	(22)
South Africa	0.899	(53)	Greece	0.971	(23)
Egypt	0.878	(55)	Sweden	0.969	(24)
Angola	0.837	(63)	Ireland	0.969	(25)
Côte d'Ivoire	0.755	(70)	Czechia	0.964	(27)
Nigeria	0.649	(75)	Croatia	0.960	(29)
Ghana	0.628	(77)	Finland	0.949	(31)
Asia	**0.883**		Slovakia	0.949	(32)
Singapore	1.000	(1)	Lithuania	0.933	(38)
Bahrain	0.995	(2)	Poland	0.925	(40)
Japan	0.993	(3)	North Macedonia	0.914	(47)
United Arab Emirates	0.990	(5)	Latvia	0.902	(52)
Korea	0.985	(8)	Bulgaria	0.861	(57)
Israel	0.985	(9)	Russia	0.814	(65)
Cyprus	0.966	(26)	Ukraine	0.757	(69)
Oman	0.961	(28)	**North America**	**0.873**	
Jordan	0.941	(35)	U.S.A.	0.982	(13)
Malaysia	0.936	(36)	Trinidad and Tobago	0.978	(20)
Turkey	0.933	(37)	Mexico	0.957	(30)
Saudi Arabia	0.920	(43)	Canada	0.943	(34)
Sri Lanka	0.842	(62)	Dominican Republic	0.915	(46)
Philippines	0.822	(64)	Jamaica	0.912	(49)
China	0.777	(66)	El Salvador	0.911	(50)
Indonesia	0.776	(67)	Panama	0.869	(56)
Thailand	0.776	(68)	Costa Rica	0.854	(59)
Viet Nam	0.707	(71)	Guatemala	0.676	(73)
Pakistan	0.681	(72)	Belize	0.606	(78)
India	0.667	(74)	**Oceania**	**0.815**	
Europe	**0.950**		Australia	0.948	(33)
United Kingdom	0.992	(4)	New Zealand	0.851	(60)
Belgium	0.990	(6)	Fiji	0.645	(76)
Germany	0.988	(7)	**South America**	**0.858**	
Malta	0.985	(10)	Uruguay	0.926	(39)
Netherlands	0.984	(11)	Argentina	0.921	(42)
Italy	0.983	(12)	Chile	0.916	(44)
Switzerland	0.982	(14)	Venezuela	0.906	(51)
France	0.981	(15)	Peru	0.898	(54)
Austria	0.981	(16)	Colombia	0.859	(58)
Portugal	0.980	(17)	Brazil	0.847	(61)
			Ecuador	0.596	(79)

Note: The table shows the wealth-share of non-natural capital by country. Global rank within the sample is shown in parentheses, where higher ranks correspond to a greater non-natural capital share. The share of renewable natural capital is averaged over the three years 1995, 2000, and 2005, for which data is available through the ND-GAIN database.

Table A.7: Correlation of Wealth-Share of Non-Natural Capital

	(1)	(2)	(3)	(4)
(1) Wealth-Share Non-Natural Capital in 1995	1.00			
(2) Wealth-Share Non-Natural Capital in 2000	0.90	1.00		
(3) Wealth-Share Non-Natural Capital in 2005	0.87	0.92	1.00	
(4) Wealth-Share Non-Natural Capital-Avg	0.96	0.98	0.96	1.00

Note: The table displays the correlation between the wealth-share of non-natural capital across the 79 countries in our regression sample for the years 1995, 2000, 2005, and the average of these three years.

Table A.8: Summary Statistics

	Mean	SD	p5	p25	p50	p75	p95
Regression Sample (N=385,861)							
CDS spread level (bps)	219.94	311.12	6.50	42.33	125.92	284.79	727.43
Absolute Change in CDS spread level (weekly, bps)	0.159	19.500	-23.444	-2.875	0.000	2.299	24.172
% Change in CDS spread (weekly)	0.416	8.947	-12.102	-2.871	0.000	2.504	14.925
Tenor							
1Y (as % of sample)	17.7						
5Y (as % of sample)	18.9						
10Y (as % of sample)	18.2						
15Y (as % of sample)	15.0						
20Y (as % of sample)	15.3						
30Y (as % of sample)	14.8						
Biodiversity News (standardized)	0.037	1.046	-1.394	-0.598	-0.102	0.556	1.822
Biodiversity Destruction Score (standardized)	0.122	0.911	-2.740	-0.079	0.349	0.624	1.034
Across-Family Dispersion of Habitat Destruction (standardized)	-0.043	0.949	-0.827	-0.582	-0.336	0.040	1.860
Wealth-Share of Non-Natural Capital (standardized)	0.113	0.851	-1.980	-0.302	0.368	0.789	0.900
Biodiversity - Country Level (N=79)							
Biodiversity Destruction Score	31.51	11.61	19.50	24.50	28.29	33.81	65.57
Biodiversity Destruction Score in 2022	30.57	13.00	16.39	23.28	27.38	33.06	66.83
Biodiversity Destruction Score (standardized)	0.000	1.000	-2.933	-0.198	0.277	0.603	1.034
Dispersion of Habitat Destruction - Country Level (N=79)							
Across-Family Dispersion of Habitat Destruction	3.135	2.913	0.725	1.518	2.237	3.338	11.886
Across-Family Dispersion of Habitat Destruction (standardized)	0.000	1.000	-0.827	-0.555	-0.308	0.070	3.004
Non-Natural Capital Share - Country Level (N=79)							
Wealth-Share of Non-Natural Capital	0.893	0.107	0.645	0.851	0.925	0.978	0.992
Wealth-Share of Non-Natural Capital (standardized)	-0.000	1.000	-2.313	-0.394	0.301	0.789	0.924

Note: The table presents summary statistics of our regression sample. The top part shows summary statistics of our regression sample of weekly changes in CDS spreads as described in section 3.2 and section A. "CDS spread level (bps)" is the absolute CDS spread in basis points, winsorized at 1% at the top and bottom. "Change in CDS spread level (weekly)" is the change in CDS spread from the prior week, expressed in basis points and winsorized at 1% at the top and bottom. "% Change in CDS spread (weekly)" is the percentage change in the CDS spread from the prior week, winsorized at 1% at the top and bottom. "Biodiversity News (AR(1) Residuals)" are the AR(1) residuals of an index measuring coverage of biodiversity loss in the New York Times, as produced by Giglio, Kelly and Stroebel (2021). "Biodiversity Destruction Score" includes the indicators for the change in biological diversity that has occurred in a country and for the amount of suitable habitat remaining for each species from the EPI's biodiversity and habitat category. In addition, it includes indicators on ecosystem services (loss in tree cover, grassland and wetlands) and fisheries. These indicators are available in 2022 and as a baseline measure around 2012. "Across-Family Dispersion of Habitat Destruction" is the across-family standard deviation of average habitat loss by family. "Wealth-Share of Non-Natural Capital" is the share of a country's wealth that is not derived from renewable natural capital, based on the World Bank's wealth accounting data. We standardize the "Biodiversity News", "Biodiversity Destruction Score", "Wealth-Share of Non-Natural Capital" and "Across-Family Dispersion of Habitat Destruction" to have mean zero and standard deviation of 1 across all countries in our sample. However, in the regression sample, the observation weighted mean and standard deviation differ slightly since the sample is unbalanced across maturities and time.

Table A.9: Correlation Between Measures of Biodiversity Reliance and Degradation

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
(1) Biodiversity Destruction Score-Avg	1.00								
(2) Biodiversity Destruction Score-Baseline	0.95	1.00							
(3) Biodiversity Destruction Score-2022	0.96	0.83	1.00						
(4) Biodiversity Destruction Score (No Ecosystem)-Avg	0.52	0.49	0.51	1.00					
(5) Environmental Vulnerability Index	0.13	0.11	0.14	0.51	1.00				
(6) Across-Family Dispersion of Area Scores	0.02	-0.00	0.03	-0.06	-0.10	1.00			
(7) Across-Suborder Dispersion of Area Scores	-0.07	-0.10	-0.04	-0.15	-0.07	0.89	1.00		
(8) Across-Family Dispersion of Habitat Scores	-0.09	-0.14	-0.03	-0.15	-0.16	0.62	0.63	1.00	
(9) Wealth-Share of Non-Natural Capital	-0.13	-0.10	-0.15	-0.08	0.13	-0.22	-0.21	-0.29	1.00

Note: The table shows the correlation between our measures of biodiversity reliance and degradation. "Biodiversity Destruction Score" includes indicators for the changes in biological diversity within a country and for the amount of suitable habitat remaining for each species from the biodiversity and habitat category, as well as indicators on ecosystem services (loss in tree cover, grassland and wetlands) and fisheries. This score is available for 2022, a baseline from approximately a decade earlier, and an "Avg" score, which represents the average of the two time periods. "Biodiversity Destruction Score (No Ecosystem)" only includes the indicators for the change in biological diversity that has occurred in a country and for the amount of suitable habitat remaining for each species from the biodiversity and habitat category, averaged over 2022 and the baseline. The "Environmental Vulnerability Index" was devised by the South Pacific Applied Geoscience Commission (SOPAC) with the UN Environment Program and their partners (Kaly, Pratt and Mitchell, 2004) to gauge a country's vulnerability to environmental hazards. The "Across-Family Dispersion of Area Scores" is the across-family standard deviation of within-family average species area scores, provided by the Map of Life (Jetz, McPherson and Guralnick, 2012). The "Across-Suborder Dispersion of Area Scores" uses the standard deviation across suborders instead, and the "Across-Family Dispersion of Habitat Scores" follows the same method but applies habitat scores, also provided by the Map of Life. The "Wealth-Share of Non-Natural Capital" is the share of non-natural capital of a country's total wealth, obtained from the ND-GAIN database (Notre Dame Global Adaptation Initiative, 2025), based on data provided by the World Bank in 2011.

Table A.10: CDS Spreads Exposure to Negative Biodiversity News By Country

	CDS Spreads Exposure to Biodiversity News									
	Biodiversity Destruction	**Across-Family Dispersion**	**Non-Natural Capital Share**	**Country Exposure**	**Exposure Rank**		**Biodiversity Destruction**	**Across-Family Dispersion**	**Non-Natural Capital Share**	**Country Exposure**	**Exposure Rank**
Malaysia	1.265	3.825	0.397	2.964	(1)	Costa Rica	0.603	-0.029	-0.367	0.154	(40)
Singapore	-1.460	4.172	0.996	1.582	(2)	Bahrain	-3.042	3.624	0.951	0.146	(41)
Portugal	1.311	-0.206	0.811	1.462	(3)	North Macedonia	0.261	-0.442	0.194	0.132	(42)
U.S.A.	0.746	0.656	0.832	1.460	(4)	New Zealand	0.632	-0.133	-0.394	0.107	(43)
Indonesia	1.029	3.004	-1.089	1.314	(5)	Thailand	0.847	0.658	-1.095	0.105	(44)
Argentina	0.790	0.914	0.258	1.184	(6)	Norway	-0.715	0.082	0.784	0.099	(45)
Uruguay	1.304	-0.170	0.303	1.096	(7)	Israel	-0.577	-0.336	0.854	0.059	(46)
Belgium	0.801	-0.353	0.900	1.090	(8)	Croatia	-0.053	-0.843	0.622	0.038	(47)
Sweden	0.223	0.773	0.707	1.040	(9)	Colombia	0.349	0.040	-0.320	0.036	(48)
Korea	0.554	-0.064	0.860	1.012	(10)	Guatemala	0.892	1.860	-2.025	-0.003	(49)
Spain	0.932	-0.643	0.781	0.964	(11)	Latvia	-0.118	0.021	0.086	-0.012	(50)
Trinidad and Tobago	0.580	-0.107	0.789	0.959	(12)	Morocco	0.039	-0.450	0.193	-0.034	(51)
Netherlands	0.639	-0.523	0.851	0.858	(13)	Brazil	0.365	-0.002	-0.434	-0.057	(52)
Denmark	0.771	-0.831	0.799	0.774	(14)	Dominican Republic	-0.079	-0.486	0.203	-0.129	(53)
United Kingdom	0.563	-0.783	0.924	0.738	(15)	Switzerland	-0.704	-0.627	0.825	-0.188	(54)
Australia	0.490	-0.060	0.509	0.707	(16)	China	0.285	0.816	-1.085	-0.224	(55)
Ireland	0.635	-0.648	0.706	0.690	(17)	Venezuela	-0.276	-0.538	0.118	-0.359	(56)
France	0.513	-0.648	0.818	0.685	(18)	Philippines	-0.093	0.205	-0.667	-0.468	(57)
Cyprus	0.377	-0.305	0.683	0.642	(19)	Russia	0.421	-0.557	-0.738	-0.495	(58)
Mexico	0.149	0.194	0.590	0.635	(20)	Peru	-0.504	-0.368	0.043	-0.503	(59)
Japan	0.194	-0.436	0.932	0.634	(21)	Viet Nam	0.627	0.671	-1.735	-0.524	(60)
Italy	0.371	-0.728	0.834	0.557	(22)	Malta	-1.648	-0.021	0.852	-0.578	(61)
Germany	0.261	-0.713	0.882	0.518	(23)	Oman	-1.155	-0.597	0.629	-0.648	(62)
Finland	-0.266	0.534	0.521	0.437	(24)	Bulgaria	-0.198	-0.667	-0.302	-0.673	(63)
Canada	0.288	-0.308	0.465	0.414	(25)	Angola	-0.249	-0.460	-0.526	-0.782	(64)
Czechia	0.259	-0.582	0.661	0.413	(26)	Egypt	-0.940	0.011	-0.144	-0.786	(65)
Greece	0.335	-0.827	0.723	0.403	(27)	Sri Lanka	-0.351	-0.524	-0.479	-0.850	(66)
Turkey	0.624	-0.719	0.372	0.402	(28)	Ukraine	0.431	-0.618	-1.266	-0.908	(67)
Poland	0.688	-0.767	0.301	0.374	(29)	Ghana	1.034	-0.043	-2.474	-1.102	(68)
Austria	-0.033	-0.462	0.816	0.370	(30)	Nigeria	0.682	-0.077	-2.271	-1.222	(69)
El Salvador	0.504	-0.289	0.167	0.359	(31)	Côte d'Ivoire	-1.140	1.111	-1.289	-1.279	(70)
Chile	0.221	0.056	0.212	0.344	(32)	Belize	0.077	0.844	-2.676	-1.543	(71)
Lithuania	0.445	-0.555	0.368	0.344	(33)	India	-0.143	-0.312	-2.108	-1.810	(72)
Jamaica	0.337	-0.090	0.173	0.333	(34)	Ecuador	0.277	0.070	-2.767	-1.819	(73)
Tunisia	0.003	0.260	0.284	0.332	(35)	Iceland	-2.740	-1.076	0.808	-1.887	(74)
South Africa	0.525	-0.403	0.055	0.239	(36)	Fiji	-0.151	-0.413	-2.313	-2.014	(75)
Panama	0.583	-0.056	-0.222	0.234	(37)	United Arab Emirates	-3.344	-0.546	0.904	-2.015	(76)
Algeria	-0.070	0.130	0.206	0.161	(38)	Jordan	-2.933	-0.547	0.447	-2.054	(77)
Slovakia	0.135	-0.715	0.516	0.154	(39)	Saudi Arabia	-3.225	-0.417	0.247	-2.357	(78)
						Pakistan	-1.060	-0.408	-1.980	-2.428	(79)

Note: The table shows each country's standardized scores for biodiversity-related degradation measures, "Biodiversity Destruction Score", "'Across-Family Dispersion of Area Scores", and "Wealth-Share of Non-Natural Capital". The standardized weighted sum country-level exposure and exposure ranking of CDS spreads to negative biodiversity news is also calculated using regression coefficients from column 2 in Table 1, where lower scores and lower ranks correspond to less exposure.

Table A.11: CDS Spreads Reaction to Biodiversity News - Robustness (Imbalance Measure)

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
Biodiversity News	0.175	0.175	0.178	0.173	0.173	0.177	0.176	0.175
	(0.117)	(0.117)	(0.117)	(0.117)	(0.116)	(0.117)	(0.117)	(0.117)
Biodiversity News ×	0.076**	0.079**	0.074**	0.068**	0.080**	0.074**	0.068**	0.072**
Biodiversity Destruction Score	(0.032)	(0.033)	(0.031)	(0.032)	(0.035)	(0.032)	(0.034)	(0.031)
Biodiversity News ×	0.047***	0.040*	0.070**	0.046	0.036*	0.061***	0.041**	0.058*
Vulnerable Group Habitat Destruction Metric	(0.013)	(0.023)	(0.030)	(0.028)	(0.018)	(0.014)	(0.016)	(0.029)
Biodiversity News ×	0.077**	0.075*	0.082**	0.085**	0.079*	0.080**	0.078**	0.084**
Wealth-Share of Non-Natural Capital	(0.037)	(0.038)	(0.035)	(0.037)	(0.040)	(0.037)	(0.036)	(0.035)
Taxonomic Group	Family	Suborder	Family	Family	Family	Family	Family	Family
Map of Life Score	Area	Area	Area	Area	Habitat	Area	Area	Area
Vulnerability Metric	SD	SD	p10	Min	SD	SD	SD	SD
Year	2021	2021	2021	2021	2021	2015	2021	2021
Low Stewardship Treatment							Drop	Cap
Observations	385,829	385,829	385,829	385,829	385,829	385,829	385,829	385,829

Note: This table presents robustness checks for Table 1. Each column reports coefficients from regressions of changes in CDS spreads on AR(1) innovations of the "Biodiversity News" index, the "Biodiversity Destruction Score", and the "Wealth-Share of Non-Natural Capital". The dependent variable is the change in CDS spreads, winsorized at the 1st and 99th percentiles within each country. All regressions include country-year-tenor fixed effects. Regression (1) uses the across-family dispersion in area scores in 2021 as the biodiversity imbalance measure, as in our baseline specification. Regression (2) replaces this with the across-suborder dispersion in area scores in 2021. Regression (3) uses the 10th percentile value of area scores across families, while Regression (4) uses the minimum value of area scores across families. Regression (5) replaces area scores with habitat scores and uses their dispersion across families in 2021. Regression (6) uses the across-family dispersion in area scores in 2015 instead. Regression (7) modifies the baseline by excluding observations from countries with less than 0.05% stewardship of the species. Regression (8) further adjusts the baseline by capping area scores at 100 for species in countries with less than 0.05% stewardship. For all measures, higher scores indicate greater imbalance in biodiversity loss. The "Biodiversity Destruction Score" is our EPI-based measure, averaged across 2022 and baseline values a decade prior. This includes the indicators for the change in biological diversity that has occurred in a country and for the amount of suitable habitat remaining for each species from the EPI's biodiversity and habitat category. The "Wealth-Share of Non-Natural Capital" is the share of non-natural capital of a country's total wealth, obtained from the ND-GAIN database (Notre Dame Global Adaptation Initiative, 2025), based on data provided by the World Bank in 2011. Standard errors are in parentheses and are clustered at the country-date level. Significance levels: * ($p<0.10$), ** ($p<0.05$), *** ($p<0.01$).

Table A.12: CDS Spreads Reaction to Biodiversity News - Robustness (Mean Destruction)

	(1)	(2)	(3)	(4)	(5)	(6)	(7)
Biodiversity News	0.175	0.175	0.177	0.177	0.177	0.178	0.184
	(0.117)	(0.117)	(0.117)	(0.119)	(0.119)	(0.119)	(0.120)
Biodiversity News ×	0.076**	0.070**	0.079**	0.070***	0.067***	0.072***	0.076***
Measure of Mean Biodiversity Destruction	(0.032)	(0.033)	(0.032)	(0.021)	(0.020)	(0.022)	(0.023)
Biodiversity News ×	0.047***	0.047***	0.048***	0.052***	0.043***	0.061***	0.053***
Across-Family Dispersion of Habitat Destruction	(0.013)	(0.013)	(0.013)	(0.014)	(0.015)	(0.013)	(0.014)
Biodiversity News ×	0.077**	0.077**	0.075**	0.076**	0.079**	0.071**	0.059*
Wealth-Share of Non-Natural Capital	(0.037)	(0.037)	(0.037)	(0.036)	(0.036)	(0.036)	(0.034)
Biodiversity Destruction Measure	EPI Physical	EPI Physical	EPI Physical	EPI Regulation	EPI Regulation	EPI Regulation	EVI
Period	Avg	2022	Baseline	Avg	2022	Baseline	2004
Observations	385,829	385,829	385,829	385,829	385,829	385,829	381,703

Note: This table presents robustness checks for Table 1. Each column reports coefficients from regressions of changes in CDS spreads on AR(1) innovations of the "Biodiversity News" index, the "Across-Family Dispersion of Habitat Destruction", the "Wealth-Share of Non-Natural Capital", and different measures of biodiversity destruction. The dependent variable is the change in CDS spreads, winsorized at the 1st and 99th percentiles within each country. All regressions include country-year-tenor fixed effects. Regression (1) uses an aggregate measure of physical indicators of biodiversity destruction, averaged between 2022 and the baseline approximately 10 years earlier. Regressions (2) and (3) uses the same aggregate measure of physical indicators only in 2022 and the baseline respectively. Regression (4) instead uses an aggregate measure of regulatory changes related to biodiversity protection, averaged between 2022 and the baseline approximately 10 years earlier. Regressions (5) and (6) similarly use the same aggregate measure of regulatory indicators only in 2022 and the baseline respectively. Regression (7) replaces this with the Environmental Vulnerability Index (EVI), devised by the South Pacific Applied Geoscience Commission (SOPAC) to gauge a country's vulnerability to environmental hazards. For all measures, higher scores indicate greater degradation of biodiversity. The "Across-Family Dispersion of Area Scores" is the across-family standard deviation of within-family average species area scores, provided by the Map of Life (Jetz, McPherson and Guralnick, 2012). "Wealth-Share of Non-Natural Capital" is the share of non-natural capital of a country's total wealth, obtained from the ND-GAIN database (Notre Dame Global Adaptation Initiative, 2025), based on data provided by the World Bank in 2011. Standard errors are in parentheses and are clustered at the country-date level. Significance levels: * ($p<0.10$), ** ($p<0.05$), *** ($p<0.01$).

Table A.13: CDS Spreads Reaction to Biodiversity News - Robustness (Capital Share)

	(1)	(2)	(3)	(4)
Biodiversity News	0.175	0.174	0.178	0.177
	(0.117)	(0.117)	(0.118)	(0.118)
Biodiversity News ×	0.076**	0.072**	0.074**	0.075**
Biodiversity Destruction Score	(0.032)	(0.031)	(0.032)	(0.032)
Biodiversity News ×	0.047***	0.046***	0.043***	0.050***
Across-Family Dispersion of Habitat Destruction	(0.013)	(0.013)	(0.014)	(0.013)
Biodiversity News ×	0.077**	0.090**	0.072**	0.071*
Measure of Non-Natural Capital Share	(0.037)	(0.042)	(0.033)	(0.037)
Period	Avg	1995	2000	2005
Observations	385,829	317,863	377,926	380,353

Note: This table presents robustness checks for Table 1. Each column reports coefficients from regressions of changes in CDS spreads on AR(1) innovations of the "Biodiversity News" index, the "Biodiversity Destruction Score", the "Across-Family Dispersion of Habitat Destruction", the "Wealth-Share of Non-Natural Capital", and wealth-share of non-natural capital measured at different periods. The dependent variable is the change in CDS spreads, winsorized at the 1st and 99th percentiles within each country. All regressions include country-year-tenor fixed effects. Regression (1) uses the average wealth-share of non-natural capital across all available years for each country, obtained from the ND-GAIN database (Notre Dame Global Adaptation Initiative, 2025), based on data provided by the World Bank in 2011. Regressions (2), (3), and (4) uses the same measure, restricted to 1995, 2000, and 2005 respectively. The "Biodiversity Destruction Score" is our EPI-based measure, averaged across 2022 and baseline values a decade prior. This includes the indicators for the change in biological diversity that has occurred in a country and for the amount of suitable habitat remaining for each species from the EPI's biodiversity and habitat category. In addition, it includes indicators on ecosystem services (loss in tree cover, grassland and wetlands) and fisheries. The "Across-Family Dispersion of Area Scores" is the across-family standard deviation of within-family average species area scores, provided by the Map of Life (Jetz, McPherson and Guralnick, 2012). Standard errors are in parentheses and are clustered at the country-date level. Significance levels: * ($p<0.10$), ** ($p<0.05$), *** ($p<0.01$).

B Theoretical Appendix - Proofs

In this Appendix, we provide details for the proofs for our key results in the main body of the paper.

Proof of Proposition 1. For each function g, denote

$$E_{-g} = \left(\sum_{j \neq g} E_j^{\frac{\sigma-1}{\sigma}} \right)^{\frac{\sigma}{\sigma-1}}, \tag{A.1}$$

so that

$$E = \left[E_g^{\frac{\sigma-1}{\sigma}} + E_{-g}^{\frac{\sigma-1}{\sigma}} \right]^{\frac{\sigma}{\sigma-1}}. \tag{A.2}$$

This notation is convenient because when we vary biodiversity in function g holding other functions $j \neq g$ fixed, everything behaves as if aggregate ecosystem services E were produced by only two functions, the function of interest g, and a fictitious function "$-g$" capturing all other functions. Denote $Z_{-g} = E_{-g}^{\sigma-1/\sigma} = \sum_{j \neq g} E_j^{\sigma-1/\sigma}$. We have:

$$\frac{\partial E}{\partial S_g} = \phi_g \frac{\bar{E}_g^{\frac{\sigma-1}{\sigma}}}{\bar{S}_g} s_g^{\phi_g \frac{\sigma-1}{\sigma} - 1} \left[\bar{E}_g^{\frac{\sigma-1}{\sigma}} s_g^{\phi_g \frac{\sigma-1}{\sigma}} + E_{-g}^{\frac{\sigma-1}{\sigma}} \right]^{\frac{1}{\sigma-1}} \tag{A.3}$$

$$\frac{\partial^2 E}{\partial S_g^2} = - \frac{\bar{E}_g \phi_g Z_{-g}^{\frac{1}{\sigma}} s_g^{\phi_g} \left(\left(\bar{E}_g s_g^{\phi_g} \right)^{\frac{\sigma-1}{\sigma}} + Z_{-g}^{\frac{\sigma-1}{\sigma}} \right)^{\frac{\sigma}{\sigma-1}}}{\sigma S_g^2 \left(\bar{E}_g Z_{-g}^{\frac{1}{\sigma}} s_g^{\phi_g} + Z_{-g} \left(\bar{E}_g s_g^{\phi_g} \right)^{\frac{1}{\sigma}} \right)^2} \left[\bar{E}_g \sigma (1-\phi_g) Z_{-g}^{\frac{1}{\sigma}} s_g^{\phi_g} + Z_{-g} (\sigma(1-\phi_g) + \phi_g) \left(\bar{E}_g s_g^{\phi_g} \right)^{\frac{1}{\sigma}} \right] \tag{A.4}$$

Therefore, $\frac{\partial^2 E}{\partial S_g^2}$ is negative if the term in the bracket is positive, that is if

$$-\sigma(1-\phi_g) < \left[\sigma(1-\phi_g) + \phi_g \right] \left(\frac{\bar{E}_g s_g^{\phi_g}}{Z_{-g}} \right)^{\frac{1}{\sigma}-1},$$

which holds since $\phi_g < 1$. Since $\sigma < 1$, the term $s_g^{\phi_g \sigma-1/\sigma}$ goes to infinity as $s_g = S_g/\bar{S}_g \to 0$ and therefore, holding other functions fixed, it dominates the term in the bracket in (A.3):

$$\left[\bar{E}_g^{\frac{\sigma-1}{\sigma}} s_g^{\phi_g \frac{\sigma-1}{\sigma}} + \sum_{j \neq g}^{G} \bar{E}_j^{\frac{\sigma-1}{\sigma}} s_j^{\phi_g \frac{\sigma-1}{\sigma}} \right]^{\frac{1}{\sigma-1}} \sim \left[\bar{E}_g^{\frac{\sigma-1}{\sigma}} s_g^{\phi_g \frac{\sigma-1}{\sigma}} \right]^{\frac{1}{\sigma-1}}$$

hence

$$\begin{aligned} \frac{\partial E}{\partial S_g} &\sim \phi_g \frac{\bar{E}_g^{\frac{\sigma-1}{\sigma}}}{\bar{S}_g} s_g^{\phi_g \frac{\sigma-1}{\sigma} - 1} \left[\bar{E}_g^{\frac{\sigma-1}{\sigma}} s_g^{\phi_g \frac{\sigma-1}{\sigma}} \right]^{\frac{1}{\sigma-1}} \\ &\sim \phi_g \frac{\bar{E}_g}{\bar{S}_g} s_g^{\phi_g \frac{\sigma-1}{\sigma} - 1} s_g^{\frac{\phi_g}{\sigma}} \sim \phi_g \frac{\bar{E}_g}{\bar{S}_g} s_g^{-(1-\phi_g)}. \end{aligned}$$

Since $\phi_g < 1$ we obtain $\lim_{S_g/\bar{S}_g \to 0} \frac{\partial E}{\partial S_g} = \infty$.

Proof of Proposition 2. We denote the covariance of two variables $\boldsymbol{x} = \{x_g\}$ and $\boldsymbol{y} = \{y_g\}$ across functional groups by $\text{Cov}(x,y) = \sum_g (x_g - \frac{1}{G}\sum_j x_j)(y_g - \frac{1}{G}\sum_j y_j)$. Define for any $\boldsymbol{s} = \{s_g\}_{g=1}^G$ and $\boldsymbol{\theta} = \{\theta_g\}_{g=1}^G$ the function:

$$f_g(\boldsymbol{s}, \boldsymbol{\theta}) = \frac{s_g^{\theta_g}}{\sum_{j=1}^G s_j^{\theta_g}}.$$

For any $(\boldsymbol{s}, \boldsymbol{\theta})$ we have $\sum_g f_g(\boldsymbol{s}, \boldsymbol{\theta}) = 1$.

$$N = \sum_{g=1}^G \bar{n}_g \bar{S}_g s_g^{\alpha_g}$$
$$d\log N = \sum_{g=1}^G \frac{\bar{n}_g \bar{S}_g s_g^{\alpha_g}}{\sum_{j=1}^G \bar{n}_j \bar{S}_j s_j^{\alpha_j}} \left[d\log \bar{n}_g + \alpha_g d\log s_g \right].$$

Starting from $\bar{n}_g \bar{S}_g = \bar{N}/G$, this simplifies to

$$d\log N = \sum_{g=1}^G f_g(\boldsymbol{s}, \boldsymbol{\alpha}) \left[d\log \bar{n}_g + \alpha_g d\log s_g \right].$$

Defining

$$\omega_g = f_g(\boldsymbol{s}, \boldsymbol{\alpha}) = \frac{s_g^{\alpha_g}}{\sum_{j=1}^G s_j^{\alpha_j}}$$
$$\mu_g = f_g\left(\boldsymbol{s}, \boldsymbol{\phi}\frac{\sigma-1}{\sigma}\right) = \frac{s_g^{\phi_g \frac{\sigma-1}{\sigma}}}{\sum_{j=1}^G s_j^{\phi_j \frac{\sigma-1}{\sigma}}}$$
$$\gamma_g = \mu_g - \omega_g$$

this rewrites

$$d\log N = \sum_{g=1}^G \omega_g \left[d\log \bar{n}_g + \alpha_g d\log s_g \right].$$

Turning to $E = \left[\sum_{g=1}^{G} \left(\bar{S}_g \bar{n}_g\right)^{\frac{\sigma-1}{\sigma}} s_g^{\phi_g \frac{\sigma-1}{\sigma}}\right]^{\sigma/\sigma-1}$, this gives us the following effect:

$$\begin{aligned}
d\log E &= \sum_{g=1}^{G} \mu_g \left[d\log \bar{n}_g + \phi_g d\log s_g\right] \\
&= \sum_{g=1}^{G} \left[\gamma_g + \omega_g\right] \left[d\log \bar{n}_g + \phi_g d\log s_g\right] \\
&= \sum_{g=1}^{G} \omega_g \left[d\log \bar{n}_g + \left(\phi_g - \alpha_g + \alpha_g\right) d\log s_g\right] + \sum_{g=1}^{G} \gamma_g \left[d\log \bar{n}_g + \phi_g d\log s_g\right] \\
&= \underbrace{\sum_{g=1}^{G} \omega_g \left[d\log \bar{n}_g + \alpha_g d\log s_g\right]}_{=d\log N} + \sum_{g=1}^{G} \omega_g v_g d\log s_g + \sum_{g=1}^{G} \gamma_g \left[d\log \bar{n}_g + \phi_g d\log s_g\right]
\end{aligned}$$

where we used $\sum_g \gamma_g = 0$ and $\phi_g - \alpha_g = \frac{1}{\epsilon_g - 1}$.

Symmetric proportional shocks. Consider a symmetric proportional shock to all functions $d\log s_g = d\log s$. Then:

$$d\log N = \left[\sum_{g=1}^{G} \omega_g \alpha_g\right] d\log s,$$

and

$$\begin{aligned}
d\log E &= d\log N + \left[\sum_{g=1}^{G} \frac{\omega_g}{\epsilon_g - 1}\right] d\log s + \text{Cov}\left[\gamma_g, \phi_g\right] d\log s \\
&= \left[\sum_g \mu_g \phi_g\right] d\log s.
\end{aligned}$$

With symmetric $\phi_g = \phi$ this becomes $d\log E = \phi d\log s$.

Symmetric additive shocks. Consider a symmetric additive shock to all functions $ds_g = ds$. Then

$$d\log N = \sum_{g=1}^{G} \frac{\omega_g \alpha_g}{s_g} ds_g$$

and

$$\begin{aligned}
d\log E &= \left[\sum_{g=1}^{G} \omega_g \frac{\phi_g}{s_g}\right] ds + \text{Cov}\left[\gamma_g, \frac{\phi_g}{s_g}\right] ds \\
&= \left[\sum_g \mu_g \frac{\phi_g}{s_g}\right] ds
\end{aligned}$$

With symmetric $\phi_g = \phi$ this becomes $d\log E = \phi \left[\sum_g \frac{\mu_g}{s_g}\right] ds$.

Uniformly distributed idiosyncratic additive shocks. Decompose

$$ds_j = ds + dz_j$$

where ds is the aggregate shock common to all functions, with mean $\bar{ds}$, and dz_j is the idiosyncratic shock which we assume is uniformly distributed with mean $\bar{dz}$, that is:

$$dz_j = \begin{cases} G\bar{dz} & \text{with probability } 1/G \\ 0 & \text{otherwise} \end{cases}$$

for each g. Note that the mean $\bar{dz}$ can be non-zero (instead of having that mean absorbed into the mean of ds) since in the short run we are focusing on species loss (not offsetting gains and losses).

Then the expected effect is

$$\mathbb{E}\left[d\log E\right] = \left[\sum_{g=1}^{G} \mu_g(\boldsymbol{s})\frac{\phi_g}{s_g}\right](\bar{ds} + \bar{dz})$$

With two functions $G = 2$ we have

$$\mu_1 = \frac{s_1^{\phi_1\frac{\sigma-1}{\sigma}}}{s_1^{\phi_1\frac{\sigma-1}{\sigma}} + s_2^{\phi_2\frac{\sigma-1}{\sigma}}}, \quad \mu_2 = 1 - \mu_1$$

thus

$$\begin{aligned}
\mathbb{E}\left[d\log E\right] &= \left[\mu_1\left(\frac{\phi_1}{s_1} - \frac{\phi_2}{s_2}\right) + \frac{\phi_2}{s_2}\right]\mu \\
&= \left[\mu_1\left(\frac{\phi_1}{s_1} - \frac{\phi_2}{s_2}\right) + \omega_2\frac{\phi_2}{s_2} + \omega_1\frac{\phi_1}{s_1} + (1-\omega_2)\frac{\phi_2}{s_2} - \omega_1\frac{\phi_1}{s_1}\right]\mu \\
&= \left[\omega_1\frac{\phi_1}{s_1} + (1-\omega_1)\frac{\phi_2}{s_2}\right]\mu + \left[\gamma_1\left(\frac{\phi_1}{s_1} - \frac{\phi_2}{s_2}\right)\right]\mu,
\end{aligned}$$

where

$$\mu = \bar{ds} + \bar{dz}.$$

Proof of Proposition 3. The first-order optimality condition with respect to physical capital K_1 is

$$\begin{aligned}
\frac{1}{Y_0 - K_1} &= \frac{\beta}{Y_1}F_{K,1} \\
\frac{K_1}{Y_0 - K_1} &= \beta\eta_{K,1}
\end{aligned}$$

therefore the optimal savings rate in physical capital is

$$\rho^* \equiv \frac{K_1^*}{Y_0} = \frac{\beta\eta_{K,1}}{1 + \beta\eta_{K,1}}.$$

The first-order optimality condition with respect to u is

$$(1-u)\frac{LF_{L,0}}{Y_0-K_1} = \frac{\beta}{Y_1}F_{E,1}\frac{dE_1}{d\log(1-u)}$$
$$(1-u)\frac{Y_0}{Y_0-K_1} = \frac{\beta\eta_{E,1}}{\eta_{L,0}}\frac{d\log E_1}{d\log(1-u)},$$

hence the optimal conservation satisfies

$$1-u^* = \frac{Y_0-K_1^*}{Y_0}\frac{\beta\eta_{E,1}}{\eta_{L,0}}\frac{d\log E_1}{d\log(1-u)}.$$

The optimality condition with respect to K_1 implies

$$\frac{Y_0-K_1^*}{Y_0} = \frac{1}{1+\beta\eta_{K,1}}$$

therefore

$$1-u^* = \Lambda\frac{d\log E_1}{d\log(1-u)}$$

where

$$\Lambda = \frac{\beta\eta_{E,1}}{\eta_{L,0}\left(1+\beta\eta_{K,1}\right)}.$$

Differentiating

$$\begin{aligned}\log E_1 &= \frac{\sigma}{\sigma-1}\log\left(\sum_g\left[\bar{n}_{g,0}(1-u)\left[s_{g,0}-\delta u\right]^{\phi_g}\right]^{\frac{\sigma-1}{\sigma}}\right)\\ &= \log(1-u)+\frac{\sigma}{\sigma-1}\log\left(\sum_g\left[\bar{n}_{g,0}\left[s_{g,0}-\delta u\right]^{\phi_g}\right]^{\frac{\sigma-1}{\sigma}}\right)\end{aligned}$$

yields

$$\frac{d\log E_1}{d\log(1-u)} = 1+\delta(1-u)\mathcal{F}(\boldsymbol{s}_1)$$

hence we obtain at any interior optimum

$$1-u^* = \frac{\Lambda}{1-\Lambda\delta\mathcal{F}(\boldsymbol{s}_0-\delta u^*\mathbf{1})}. \tag{A.5}$$

The comparative statics of the optimal conservation $1-u^*$ with respect to a_E, β, δ, $\boldsymbol{s}_0$ follow from the fact that the left-hand side of (A.5) is decreasing in u, and the right-hand side is decreasing in $\boldsymbol{s}_0$ (i.e., in each $s_{g,0}$) and increasing in u, δ, β and a_E.

To see the role of initial capital K_0, we need to use the two equations in two unknowns (u, X_1):

$$\left[X_1^{\frac{1}{\xi}-1} + 1 + \beta\theta\right] X_1^{\frac{1}{\theta}} = \frac{\beta\theta\left(\bar{u}L\right)^{\frac{1-\theta}{\theta}}}{E_1(u)^{\frac{1}{\theta}}} F(K_0, uL, s_0) \tag{A.6}$$

$$1 - u = \frac{\Lambda(u, X_1)}{1 - \Lambda(u, X_1)\delta\mathcal{F}\left(\boldsymbol{s}_0 - \delta u\mathbf{1}\right)}, \tag{A.7}$$

where $X_1 = \frac{K_1^\theta(\bar{u}L)^{1-\theta}}{E_1}$. The left-hand side of (A.6) is increasing in X_1 (since $\xi < 1$) and the right-hand side is increasing in u and K_0. Therefore we can invert (A.6) to get X_1 increasing in u and K_0. Then the right-hand side of the second equation (A.7) is decreasing in u and increasing in X_1 and thus in K_0, while the left-hand side is increasing in u. Therefore a higher K_0 implies a lower optimal land use u.

Proof of Proposition 4. The first-order optimality condition with respect to each u_g is

$$\frac{L_g}{L}(1 - u_g) = \Lambda \frac{\partial \log E_1}{\partial \log(1 - u_g)}.$$

Taking the ratio of optimality conditions for two functions g and h yields

$$\frac{1 - u_g}{1 - u_h} = \frac{L_h}{L_g} \frac{\partial \log E_1 / \partial \log(1 - u_g)}{\partial \log E_1 / \partial \log(1 - u_h)},$$

but now

$$E_1 = \left\{ \sum_g \left[\bar{n}_g (1 - u_g) \left[s_{g,0} - h_g(s_{g,0}, u_g) \right]^{\phi_g} \right]^{\frac{\sigma-1}{\sigma}} \right\}^{\frac{\sigma}{\sigma-1}}$$

$$\frac{\partial \log E_1}{\partial \log(1 - u_g)} = \frac{\left[\bar{n}_g (1 - u_g) s_{g,1}(s_{g,0}, u_g)^{\phi_g} \right]^{\frac{\sigma-1}{\sigma}}}{\sum_j \left[\bar{n}_j (1 - u_j) \left[s_{j,1}(s_{j,0}, u_j) \right]^{\phi_j} \right]^{\frac{\sigma-1}{\sigma}}} \left\{ 1 + \phi_g \frac{\partial \log s_{g,1}}{\partial \log(1 - u_g)} \right\}$$

$$\frac{\partial \log E_1}{\partial \log(1 - u_g)} = \mu_g \left\{ 1 + (1 - u_g) \frac{\phi_g}{s_{g,1}} \delta \right\}.$$

Therefore for each g

$$1 - u_g = \Lambda \left(\frac{\mu_g(\boldsymbol{s}_1)}{L_g / L} \right) \left\{ 1 + (1 - u_g) \frac{\phi_g}{s_{g,1}} \delta \right\},$$

which can be rewritten as

$$\frac{\mu_g(\boldsymbol{s}_1)}{1 - u_g} = \frac{L_g}{L} \frac{1 - \Lambda\delta\mathcal{F}(\boldsymbol{s}_1)}{\Lambda} + \delta \left[\frac{L_g}{L} \mathcal{F}(\boldsymbol{s}_1) - \phi \frac{\mu_g(\boldsymbol{s}_1)}{s_{g,1}} \right],$$

hence summing over g

$$\frac{1}{\sum_g \frac{\mu_g(\boldsymbol{s}_1)}{1 - u_g}} = \frac{\Lambda}{1 - \Lambda\delta\mathcal{F}(\boldsymbol{s}_1)}.$$

B.1 Calibration of Elasticity of Substitution σ

We illustrate how to calibrate the elasticity of substitution σ between ecosystem functions, using as example the empirical findings from Sutter and Albrecht (2016). They report that individual improvements in pollination and pest control increased yield by approximately 6-7% each, while joint improvements led to a 23% increase. We match these patterns using our CES specification from equation (7). Specifically, starting from a baseline where all functions are at level $\bar{E}$ and considering improvements in the first two functions E_1 and E_2, we calculate:

$$\begin{aligned} \text{Single effect: } & E(\bar{E} + \Delta E, \bar{E}, \bar{E}) - E(\bar{E}, \bar{E}, \bar{E}) \\ \text{Joint effect: } & E(\bar{E} + \Delta E, \bar{E} + \Delta E, \bar{E}) - E(\bar{E}, \bar{E}, \bar{E}) \end{aligned}$$

where ΔE is chosen to generate a 23% increase in total ecosystem services under joint improvement. The ratio of single to average joint effects in our CES specification is then compared to the empirical ratio of approximately $6.5/23 \approx 0.28$. This calibration suggests $\sigma \approx 0.1$.

B.2 First-order approximation of fragility

Define

$$\sum_{g=1}^{G} s_g^x = \bar{s}^x \sum_{g=1}^{G} (1+\delta_g)^x, \quad \sum_{g=1}^{G} s_g^{x-1} = \bar{s}^{x-1} \sum_{g=1}^{G} (1+\delta_g)^{x-1},$$

where $\bar{s} = \frac{1}{G}\sum_{g=1}^{G} s_g$ is the cross-functional average of s_g, and

$$s_g = \bar{s}(1+\delta_g), \quad \sum_{g=1}^{G} \delta_g = 0.$$

Hence

$$\mathcal{F}(\mathbf{s}) = \frac{\phi}{\bar{s}} \frac{\frac{1}{G}\sum_{g=1}^{G}(1+\delta_g)^{x-1}}{\frac{1}{G}\sum_{h=1}^{G}(1+\delta_h)^{x}}.$$

When $\delta_g = 0$ for all g—that is, s_g are perfectly uniform—we have $(1+\delta_g)^x = 1$ and thus $\mathcal{F}(\mathbf{s}) = \frac{\phi}{\bar{s}}$. We now expand around small $\{\delta_g\}$ to obtain the leading-order effect of *dispersion* in $\{s_g\}$. For each g, write

$$(1+\delta_g)^x \approx 1 + x\delta_g + \tfrac{x(x-1)}{2}\delta_g^2, \qquad (1+\delta_g)^{x-1} \approx 1 + (x-1)\delta_g + \tfrac{(x-1)(x-2)}{2}\delta_g^2.$$

Define $\mathrm{Var}(\delta) = \frac{1}{G}\sum_g \delta_g^2$. Then

$$A(\delta) \equiv \tfrac{1}{G}\sum_{g=1}^{G}(1+\delta_g)^x \approx 1 + \tfrac{x(x-1)}{2}\mathrm{Var}(\delta),$$

$$B(\delta) \equiv \tfrac{1}{G}\sum_{g=1}^{G}(1+\delta_g)^{x-1} \approx 1 + \tfrac{(x-1)(x-2)}{2}\mathrm{Var}(\delta).$$

Hence

$$\mathcal{F}(\mathbf{s}) = \frac{\phi}{\bar{s}} \frac{B(\delta)}{A(\delta)} \approx \frac{\phi}{\bar{s}} \Big[1 + \left(\frac{(x-1)(x-2)}{2} - \frac{x(x-1)}{2} \right) \mathrm{Var}(\delta) \Big].$$

Substituting

$$\frac{(x-1)(x-2)}{2} - \frac{x(x-1)}{2} = -(x-1) = 1 - \phi + \frac{\phi}{\sigma}$$

yields

$$\mathcal{F}(\mathbf{s}) \approx \frac{\phi}{\bar{s}} \Big[1 + \left(1 - \phi + \frac{\phi}{\sigma} \right) \mathrm{Var}(\delta) \Big].$$

C Theoretical Appendix — Model Extensions and Relation to Existing Work

In this Appendix, we discuss extensions of the model, and provide more detailed discussions of how our modeling approach relates to prior work.

C.1 Extension to within-function asymmetry of abundance

While our expression for the production of each ecosystem function in equation (4) is derived under the simplifying assumption of symmetry across the populations of species within the function, it generalizes to considering within-function variation in populations via a measure of biodiversity introduced by Hill (1973). Specifically, the *Hill number of order q*—also sometimes referred to as the "effective number of species"—is defined as:

$$D_q(\boldsymbol{p}) = \left(\sum_{i=1}^{S_g} p_{i,g}^q \right)^{\frac{1}{1-q}},$$

where $p_{i,g} = n_{i,g} / (\sum_{i=1}^{S_g} n_{i,g})$ is the relative abundance of species i within its functional group.[24] Empirical work in ecology routinely uses Hill numbers to measure biodiversity (Ohlmann et al., 2019), while theoretical work has provided axiomatic foundations for Hill numbers, showing that they are the only class of diversity indices obeying a set of desirable properties (Leinster, 2021).

In the special case of symmetric relative abundances in our baseline model, $p_{i,g} = 1/S_g$, the Hill number coincides with the number of species, that is, $D_q(\boldsymbol{p}) = S_g$, for any order q. Our results considering variation in the number of species S_g can be extended to allow for heterogeneity of abundance within functions. For instance, we can write a generalized version of equation (4) as:

$$E_g = \underbrace{\left[D_{\frac{\epsilon_g - 1}{\epsilon_g}}(\boldsymbol{p}) \right]^{\frac{1}{\epsilon_g - 1}}}_{\text{Gains from Biodiversity}} \times \underbrace{N_g}_{\text{Community Abundance}},$$

where the community abundance is $N_g = \sum_{i=1}^{S_g} n_{i,g}$. In this case, a change in the distribution of relative abundances $\boldsymbol{p}$ can affect E_g even when holding N_g and the number of species S_g fixed. While such an extension may be desirable for some use cases, we focus the paper on the special case where biodiversity is fully captured by the number of species, and there is no asymmetry across species within functions.

C.2 Connection to Weitzman (1998)'s *Noah's Ark*

In one of the most prominent discussions of the economic value of biodiversity, Weitzman (1998) proposes a framework to determine optimal conservation efforts of species under a budget constraint. Specifically, the framework proposes to prioritize species i for conservation according to a criterion $R_i = U_i + D_i$ that has two parts: a species' *direct utility* U_i that does not depend on other species, and its *distinctiveness* D_i that captures its difference from other species $j \neq i$ (see also Weitzman, 1992, 1993; Metrick and Weitzman, 1998). In Weitzman (1998), distinctiveness is inversely related to a species' evolutionary overlap with other species (see Solow, Polasky and Broadus, 1993, for a similar approach).

[24] For example, the Hill number of order $q = 2$ is equal to the inverse Herfindahl-Hirschman index (inverse HHI), which is a common measure of competition (or, conversely, lack of concentration) in the context of firms.

By contrast, in our framework we can define the value of any species i in function g as $R_{i,g} = \log \frac{\partial E}{\partial S_g}$ (since we assume symmetry within functions, each of the S_g species has the same value). In our framework, a species's direct utility $U_{i,g}$ is its value if all species were perfectly substitutable ($\epsilon_g, \sigma \to \infty$), so that distinctiveness would go to zero. This yields a definition of direct utility $U_{i,g} = \log \frac{a_g \alpha_g \bar{E}_g}{\frac{1-\alpha_g}{s_g} \bar{S}_g}$ and allows to decompose $R_{i,g} = U_{i,g} + D_{i,g}$ where distinctiveness is given by:

$$D_{i,g} = \log\left(1 + \frac{1}{\alpha_g(\epsilon_g - 1)}\right) + \alpha_g\left[\frac{1}{\alpha_g(\epsilon_g - 1)}\left(\frac{1}{\sigma} - 1\right) + \frac{1}{\sigma}\right]\log\left(\frac{1}{s_g}\right) - \frac{1}{\sigma}\log \bar{E}_g,$$

and we omit a term $\frac{1}{\sigma}\log E$ that is common to all species. A lower σ increases distinctiveness, because by increasing the curvature of the biodiversity-productivity relation, it sharpens differences between functions that have experienced differential losses; for similar reasons, it increases it more for species in functions with low s_g and low substitutability ϵ_g.

C.3 The Rise of Fragility and Biodiversity Risk over Time

Over time, as ecosystems are hit by species loss, the fragility of ecosystems increases, particularly if species loss has created imbalances in biodiversity across functions. Indeed, even if at any point in time the risk of species loss is uniformly distributed across functions, the expected dispersion in s grows over time, thereby amplifying the fragility to future biodiversity shocks. To see this, suppose again that $\phi_g = \phi$ is the same across functions.

Consider the impact of a sequence of species losses, where every period only one function is hit, with $ds_g = -G\delta < 0$ and $ds_j = 0$ for $j \neq g$, with a uniform probability $1/G$ for each function.[25] Then:

(i) The expected effect of a date-t species loss shock on ecosystem service production, normalized by $-\delta$, is given by the expected fragility at date t, and is increasing over time.

$$-\frac{1}{\delta}\mathbb{E}_0\left[d\log E(t)\right] = \mathbb{E}_0\left[\mathcal{F}(\boldsymbol{s}(t))\right].$$

(ii) Define forward biodiversity risk, or simply **biodiversity risk**, as the expected standard deviation of the response $d\log E(t)$ to a date-t species loss shock, normalized by δ. Then biodiversity risk also increases over time.

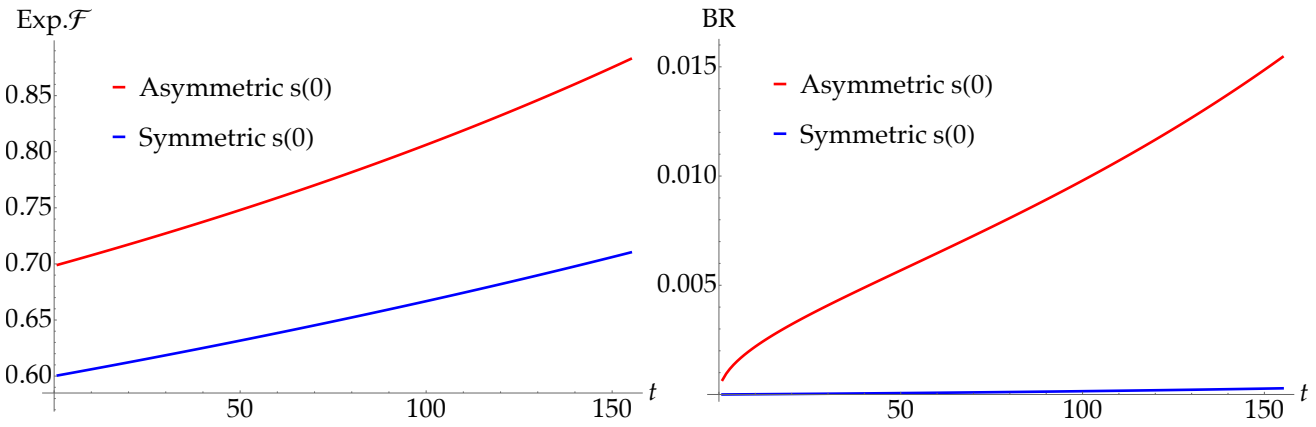
$$\mathrm{BR}(t) = \frac{1}{\delta}\sqrt{\mathbb{E}_0\left[\mathrm{Var}(d\log E(t))\right]} \tag{A.8}$$

$$= \sqrt{\mathbb{E}_0\left[\mathrm{Var}(\mathcal{F}(\boldsymbol{s}(t)))\right]} \tag{A.9}$$

Part (i) states that expected fragility increases over time. This is driven by the three forces described in equation (12): the average number of species s_g falls in all functions, which increases both $\sum_{g=1}^{G}\omega_g\frac{\alpha_g}{s_g}$ and $\sum_{g=1}^{G}\omega_g\frac{v_g}{s_g}$, and imbalances in biodiversity are expected to rise simply because some functional groups will randomly face larger species losses than others. Even though we assume that the shocks follow a

[25] In this specification, δ is the per-period average species loss expressed as a share of the maximal number of species $\bar{S}$ (e.g., $\delta = 1/\bar{S}$ corresponds to losing one species per period). Community abundance declines deterministically as $N(t) = N(0) - \delta t$.

Figure C.5: Fragility and Biodiversity Risk over Time.



Note: Panel (A) shows the expected fragility $\mathcal{F}$ at date t. Panel (B) shows biodiversity risk BR at date t. In blue, "symmetric $s(0)$" means $s_1(0) = s_2(0) = 1/2$. In red, "asymmetric $s(0)$" means $s_1(0) = 1/4, s_2(0) = 3/4$. Other parameters that are common across panels: $\sigma = 0.5$, $\phi = 0.3$, $\mu = 1/1000$.

stationary process (i.e., the number of species lost in each period remains stable), the depletion of natural capital makes the ecosystem more sensitive to the same shocks as time unfolds.

Part (ii) shows that the increased fragility also translates into an increasing expected range of potential effects on ecosystem service provision from a given species loss, as measured by the a larger expected dispersion in the response to shocks $d \log E(t)$. Thus *biodiversity risk*, expressed in terms of the risk to ecosystem services production, is expected to rise over time even when holding the process of species loss fixed. Intuitively, at any point in time, the best case scenario happens if species loss is concentrated in functions with relatively high biodiversity, as then the realized aggregate effect can be smaller than implied by the total loss in biomass. Conversely, the worst case scenario is when a shock hits a function that already features low biodiversity. As time unfolds, the difference between the best and worst outcomes following a given shock are expected to increase. Note that $\text{BR}(t)$ as defined in equation (A.9) is a measure of *forward* risk, i.e., the expected dispersion of $d \log E(t)$, and not the expected dispersion in $E(t)$ itself, which would capture a *cumulative* risk that would rise over time even in a world without any role for biodiversity (i.e., such that $\sigma, \epsilon_g \to \infty$), simply through the accumulation of shocks.

Figure C.5 considers an example with $G = 2$ functions and shows how fragility and biodiversity risk are expected to increase over time, contrasting what happens when the ecosystem starts from a symmetric initial point $s_1(0) = s_2(0) = 1/2$ versus when the ecosystem starts from an asymmetric initial point $s_1(0) = 1/4$ and $s_2(0) = 3/4$. Therefore total past species losses are the same (starting from a total number of species half of its maximal number $2\bar{S}$), but in the asymmetric case losses were concentrated in function 1. In both cases, fragility and biodiversity risk grow over time, but when initial conditions are asymmetric they both start from higher levels and grow much more quickly over time.

Summary. Our model yields a tractable measure of the fragility of ecosystem services and how it is affected by species loss over time. Ecosystem fragility captures three conceptually distinct ways in which

species loss affects ecosystem services production: (i) a direct reduction in community abundance (i.e., population or biomass); (ii) a within-function impact of species loss through the within-function "niche differentiation" mechanism; and (iii) changes in imbalances in biodiversity, capturing the amplification due to imbalances in species loss across functions and how it interacts with the complementarity ($\sigma < 1$). We show that the presence of random idiosyncratic shocks naturally increases the dispersion of realized species loss across functions—even if we start from a symmetric point—and we highlight how this increases both expected fragility and biodiversity risk over time.

C.4 Closed-Form Expression for Λ

With our production function (16) we have

$$\Lambda = \frac{a_E X_0^{\frac{1}{\xi}-1} + 1}{1-\theta} \cdot \frac{\beta a_E X_1^{\frac{1}{\xi}-1}}{a_E X_1^{\frac{1}{\xi}-1} + 1 + \beta\theta}$$

where $X_t = K_t^\theta (u_t L)^{1-\theta} / E_t$.

C.5 Analytical Example of Optimal Conservation Policy

In the limit of no substitutability between functions $\sigma \to 0$, optimal land conservation is

$$1 - u^* = \left[\underline{s}_{g,0} - \delta\left(1 + \Lambda(1+\phi)\right)\right] \frac{\sqrt{1 + \frac{4\Lambda\delta(\underline{s}_{g,0}-\delta)}{\left[\underline{s}_{g,0}-\delta(1+\Lambda(1+\phi))\right]^2}} - 1}{2\delta}$$

where

$$\underline{s}_{g,0} = \min_g s_{g,0}$$

is the most critical ecosystem function.

Note that with perfect symmetry $\phi_g = \phi$ for all g and initial biodiversity loss is symmetric across functions ($s_{0,g} = s_0$ for all g), then we obtain the same analytical expression for optimal land conservation (using the notation s_0 instead of $\underline{s}_{g,0}$ since all functions are symmetric) for general values of $\sigma > 0$

$$1 - u^* = \left[s_0 - \delta\left(1 + \Lambda(1+\phi)\right)\right] \frac{\sqrt{1 + \frac{4\Lambda\delta(s_0-\delta)}{\left[s_0-\delta(1+\Lambda(1+\phi))\right]^2}} - 1}{2\delta}. \tag{A.10}$$

C.6 Targeted Land Use

A key challenge specific to biodiversity relative to the extraction of other exhaustible resources is that the richness of ecosystem services and their interactions makes it difficult to fine-tune land use to preserve the most critical ecosystem functions. In our baseline model, we focus on an extreme case where land use is one-dimensional, so that it cannot be targeted at all. There may be settings, however, where it is possible to at least partially target land use, for instance if we think of functions as also capturing ecosystems in different locations.

Consider now the other polar case, where the planner can choose a different utilization rate u_g for

each piece of land L_g associated with ecosystem function g. Total land is $L = \sum_g L_g$ and production is:

$$Y_0 = F(K_0, \sum_g u_g L_g, E_0).$$

This means that we assume that each piece of land is perfectly substitutable from the perspective of economic production. Reality is likely to lie between the two extreme cases we study, with land use and economic activity having multiple dimensions, without being sufficiently granular to avoid spillovers on some critical ecosystem functions. The planning problem becomes

$$\max_{\{u_g\}, K_1} \log\left(F(K_0, \sum_g u_g L_g, E_0) - K_1\right) + \beta \log\left(F(K_1, \bar{u}L, E_1(\{u_g\}))\right),$$

with the following solution, which we assume to be interior for simplicity:

Proposition 4. *The vector of optimal conservation across functions satisfies*

$$\frac{1}{\sum_g \frac{\mu_g(\boldsymbol{s}_1)}{1-u_g}} = \frac{\Lambda}{1 - \Lambda\delta\mathcal{F}(\boldsymbol{s}_1)}. \tag{A.11}$$

For any pair of functions g, h, the ratio of optimal conservation satisfies:

$$\frac{1-u_g}{1-u_h} = \frac{\mu_g(\boldsymbol{s}_1)}{\mu_h(\boldsymbol{s}_1)} \cdot \frac{1 - \Lambda \frac{\mu_h(\boldsymbol{s}_1)}{L_h/L} \frac{\phi_h}{s_{h,1}} \delta}{1 - \Lambda \frac{\mu_g(\boldsymbol{s}_1)}{L_g/L} \frac{\phi_g}{s_{g,1}} \delta}.$$

Equation (A.11) is the counterpart of equation (25) in Proposition 3, but replacing the uniform land use u with the harmonic weighted-average of optimal conservation levels across functions $\left(\sum_g \mu_g(\boldsymbol{s}_1)/(1-u_g)\right)^{-1}$, with weights equal to each function's criticality μ_g (defined in Proposition 2).

Recalling that land use affects natural capital in two distinct ways, through abundance and species loss, the first term captures the fact that even without impact on biodiversity ($\delta \to 0$), or with small output effects ($\Lambda \to 0$), the optimal ratio of conservation is given by the ratio of criticalities μ, i.e., the marginal rate of substitution between functions g and h. The second channel, working through biodiversity loss ($\delta > 0$), goes in the same direction: scarcer functions should be more preserved. The design of Pigovian policies towards the conservation of natural capital should thus take into account past biodiversity loss for two reasons: first, the relative impact of land use on abundance loss (holding future biodiversity $\boldsymbol{s}_1$ fixed) depends on the criticality of each functions, and second, functions that are already critical must be protected even more once we take into account how land use affects species loss.

Intuitively, the economic gains from corrective policies can be maximized by targeting taxes and conservation efforts towards species loss in those functions with little remaining redundancy, as well as those functions whose current output is binding for overall ecosystem productivity. Conservation efforts aimed at minimizing the economic costs of biodiversity loss should aim to equalize the MRS between all pairs of functions to 1. Similarly, our findings highlight that ecosystem-wide conservation efforts should focus on locations with a higher ecosystem fragility. This identification of the economically most

meaningful conservation efforts requires a collaboration between economists and ecologists, and our general organizing framework can guide those collaborations.

C.7 Optimal Conservation With Nature in the Utility

Suppose that the date-1 utility function is

$$\log C_1 + \nu \log E_1.$$

The only change in the proof of Proposition 3 is that the optimality condition with respect to land use u becomes

$$\begin{aligned} & (1-u)\frac{LF_{L,0}}{Y_0 - K_1} = \left[\frac{\beta}{Y_1}F_{E,1} + \beta\frac{\nu}{E_1}\right]\frac{\partial E_1}{\partial \log(1-u)} \\ \Rightarrow \quad & (1-u)\frac{Y_0}{Y_0 - K_1} = \frac{\beta(\eta_{E,1}+\nu)}{\eta_{L,0}}\frac{\partial \log E_1}{\partial \log(1-u)}. \end{aligned}$$

Therefore Proposition 3 is exactly the same up to a redefinition of Λ as

$$\Lambda = \frac{\beta(\eta_{E,1}+\nu)}{\eta_{L,0}\,(1+\beta\eta_{K,1})}.$$

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