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. It follows that economic output is an increasing but concave function of species richness, and the economic cost of losing a species depends on: (i) how many redundant species remain within its ecosystem function, and (ii) how critical the affected function is for ecosystem productivity. We derive an expression for the fragility of ecosystems and economic output to further biodiversity loss, and show that it increases with both mean species losses as well as the imbalance of species losses across ecosystem functions. Consistent with the model, we illustrate that empirical measures of these components of ecosystem fragility are reflected in market assessments of risk in the cross-section of countries, which we extract from the prices of sovereign credit default swaps. We conclude by embedding our model of ecosystem services production in an intertemporal planning problem and study optimal land use when allocating land to production 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, it 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, with the pace further 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 "*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 implications for the economy and financial stability. 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,*" adding 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, noting 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, recent research by the World Bank has concluded that biodiversity losses in just three ecosystem functions—pollination, fisheries, and timber—would cost about 2.3% of global GDP (about $2.7 trillion) annually by 2030 (Johnson et al., 2021).

Given this increasing concern that nature loss—and, in particular, biodiversity and species loss[1]—might significantly disrupt economic activity, most mainstream macroeconomic models are surprisingly silent on the relationship between the two.[2] While an important strand of the literature has studied nature's contribution to economic activity and growth, this is often done by considering a monolithic stock of "natural capital" that either directly enters the production function, or that affects the productivity of other factors of production or the R&D process (Dasgupta and Heal, 1974; Stiglitz, 1974; Solow and Wan, 1976; Barbier and Markandya, 1990; Goeschl and Swanson, 2002; Lanz, Dietz and Swanson, 2018; Zhu, Smulders and de Zeeuw, 2019). While making substantial progress in highlighting various ways in which the economy might be 'embedded' in nature (using the language of Dasgupta, 2021), these approaches are generally silent on how to aggregate the totality of species into such measures of natural capital (Fenichel, Dean and Schmitz, 2024). Indeed, by abstracting from the potential interactions between different species, these models have no direct role for bio*diversity*, and provide no framework for exploring whether species vary in terms of their economic importance; whether the economic contribution of a given species is the same across different ecosystems; and which economies are most at risk from additional species loss.[3]

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[1] While the term biodiversity can capture variation across different '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 (Hooper et al., 2005).

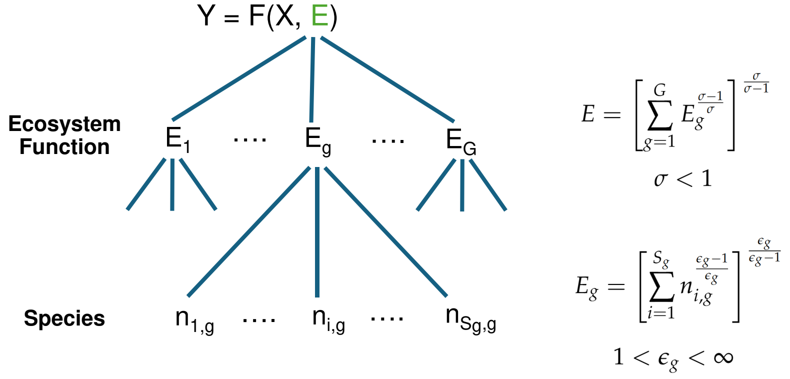
[2] This is in contrast to the more advanced work that integrates models of climate change and economic and financial activity (Nordhaus, 1991; Nordhaus and Boyer, 2003; Giglio, Kelly and Stroebel, 2021; Giglio et al., 2021; Barnett, Brock and Hansen, 2022; Barro, 2015; Weitzman, 2009). Similarly, work 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).

[3] Some researchers have considered different types of natural capital, for example within the context of specific small-scale ecological settings (e.g., multi-species fisheries, as in Yun et al., 2017). Also, the literature on sustainable development (Hartwick, 1978; Hamilton and Clemens, 1999; Arrow et al., 2012) has considered the interaction of different types of natural resources, and Dasgupta (2021) includes a separate role for provisioning and supporting ecosystem services in an aggregate production

In this paper, we fill this gap by developing a novel model of how species loss affects aggregate economic activity. Our framework explicitly specifies how different species interact to generate aggregate *ecosystem services* that enter more familiar economic production functions (see Daily, 1997; Daily et al., 2000; Chichilnisky and Heal, 1998; Heal, 2000, 2016; 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 pollination, 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 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 understand the sources of economic risks 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 (see Diaz and Cabido, 2001; Cardinale et al., 2012, and Section 1.1 for a review of this literature). Figure 1 presents a simple schematic of the model. As in prior work, aggregate ecosystem services E enter the economic production function together with other factors of production X. The production function for ecosystem services has two layers. The top layer describes how the outputs from different complementary ecosystem functions, E_g, contribute to the production of aggregate ecosystem services. The bottom layer describes how the output in each ecosystem function is produced by the interaction of multiple substitutable species, with $n_{i,g}$ capturing 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 the idea 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 (Arrow et al., 1961; Dixit and

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function. Nevertheless, these papers remain silent on how the different species contribute to the provision of the various ecosystem services, or how they interact due to their joint dependence on each other and a healthy ecosystem.

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 ecosystem function. Here, we capture the idea that there are usually multiple species playing similar functional roles (e.g., many insect species provide pollination services). After assigning each species to an ecosystem function, we model the total output of a function as another CES aggregator across the number of individual members from 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 a bigger 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, or that allow them to perform the function in different ways: for example, since different pollinator species operate at different times of the day and at different temperatures, overall pollination service production rises with the number of pollinator species.

Our model captures both the increasing and the concave natures of the within-function "biodiversity-productivity" relationship: while increases in biodiversity have positive effects on the output of an ecosystem function, the marginal benefits decline as more species are present. As a result, the loss of a species will have less severe consequences in a species-rich ecosystem relative to a biodiversity-degraded one, since the presence of many species performing similar functions in a species-rich ecosystem represents a form of diversification against the risk of species extinction. This concavity also implies that species losses have increasingly larger negative effects on both ecosystem service production and the resilience of the ecosystem to further species losses. In the extreme case, when biodiversity is sufficiently deteriorated, remaining species may become "keystone species": species whose extinction will lead to large negative effects on ecosystem output and economic activity (Frank and Sudarshan, 2024).

The concavity that arises from the interaction of species *within* each function in the bottom layer gets amplified through the interactions *across* the various complementary functions in the top layer. Even when species loss in a given function has become large enough to meaningful reduce the output of that function, this will only affect the production of aggregate ecosystem services when the function has sufficiently deteriorated to become a bottleneck in the ecosystem.[4] Therefore, through the combination of the two hierarchical layers, each introducing a different source of concavity, our model can generate substantial nonlinearities that have been discussed in the ecology and biodiversity literature (e.g., Svartzman et al., 2021; Fenichel, Gopalakrishnan and Bayasgalan, 2015).

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[4] 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 output 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.

Having specified the hierarchical structure of our production function of ecosystem services, we characterize the aggregate impact of species losses across multiple functions. Specifically, we derive a decomposition inspired by the literature on the economic effects of input misallocation across firms and sectors (Hsieh and Klenow, 2009; Baqaee and Farhi, 2019*b*). The decomposition allows us to distinguish three effects of species losses on the production of ecosystem services: (i) a direct effect of abundance loss, as members of the lost species no longer participate in the production of ecosystem services; (ii) a loss in function-level productivity conditional on abundance, coming from declines in niche differentiation; and (iii) an additional effect when losses are asymmetric across functions: because functions are complementary in the production of ecosystem services, species losses that are concentrated in a few functions are more problematic than the same total losses spread out uniformly across all functions. One contribution of our paper is thus to show how general insights from the literature on disaggregated models of the macroeconomy can be combined with parameter restrictions implied by the ecology literature to study the aggregate economic consequences of biodiversity loss.

In addition to the general decomposition of the response to an arbitrary biodiversity shock, we also derive a singular tractable measure of the *fragility* of ecosystem services. Fragility is defined as the vulnerability of aggregate ecosystem services to species losses that are uniform across functions, and combines information about the average state of biodiversity and the existing imbalances within and across functions. Since fragility captures the vulnerability of an ecosystem to future shocks, it represents a notion of *biodiversity risk* that can be brought to the data

The next step in integrating biodiversity into an economic model is to capture the role of ecosystem services in the aggregate economic production function, the F at the very top of Figure 1. We propose an economic production function that combines ecosystem services with other factors of production, such as land and capital. The relationship between biodiversity loss and economic output inherits many of the properties of the relationship between biodiversity loss and the production of aggregate ecosystem services. If ecosystem services and other factors of production are complements (as proposed by Cohen, Hepburn and Teytelboym, 2019; Dasgupta, 2021), the concavity of the relationship between biodiversity and ecosystem services is further amplified: losses of aggregate ecosystem services in response to biodiversity loss will only reduce 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. First, to provide concrete examples of such economic effects, we review several well-identified case studies of the loss of keystone species that had meaningful economic and social effects. We also discuss several instances of collapses of local ecosystems—such as the Aral Sea ecosystem collapse, and the Dust Bowls in the United States and China—that led to large-scale economic and social costs.

We also go beyond these case studies by systematically examining the aggregate effects of biodiversity loss in a cross-country setting.[5] Any study of the macroeconomic effects of biodiversity loss is complicated by two factors. First, these effects often unfold over long horizons and at low frequencies. And second, as long as biodiversity is not yet too degraded, our model suggests that biodiversity loss should

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[5] 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, 2025*a*).

largely increase the risks from future biodiversity losses (by raising ecosystem fragility) without having large effects on current macroeconomic aggregates. For these reasons, we analyze forward-looking measures of country-level *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*.

Specifically, we study the prices of sovereign credit default swaps (CDS), which reflect 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 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 modest in magnitude and 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.

We then exploit the *cross-sectional* variation in biodiversity risk exposures across countries to provide evidence for several key predictions from our model. We find that negative biodiversity news induces significant increases in CDS spreads specifically for those countries with more depleted ecosystems as captured by several distinct indicators of average ecosystem health. To explore whether *imbalances* in past biodiversity losses across functions additionally increase a country's biodiversity risk exposure, we join data from the Map of Life project (Jetz, McPherson and Guralnick, 2012), which collects species-level proxies for biodiversity losses, with taxonomic classification from the TetrapodTraits data (Moura et al., 2024), which maps each species into proxies for their ecosystem functions. Our analysis suggests that, indeed, countries with a larger *dispersion* in species losses across functions experience larger increases in CDS spreads in response to negative biodiversity news.

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 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 that have already suffered large and dispersed species losses, and, if ecosystem services and physical capital are complements in production, 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 that can be used for several policy purposes. First, it can inform the design of Pigouvian taxes on economic activities that might lead to local extinctions of species. Second, it provides a tool to think about the prioritization of conservation efforts in a world where society's willingness to pay for nature protection is finite. Third, it can be helpful to determine appropriate 'exchange rates' across 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.

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 representative 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 addition, 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.[6]

We next review insights from the ecology literature on important implications of biodiversity for ecological outcomes. A key contribution of our work is to then propose a tractable approach to modeling the aggregation of the contributions of various species to the production of E in a way that allows the integration of these insights into standard 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.

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[6] 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. Overall, our approach therefore takes an anthropocentric perspective that considers how species are useful to humans—whether directly or through increasing economic output—though it can be extended easily to also allow a valuation of species existence per se.

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 have described these interactions and interdependencies using "ecosystem networks" similar to input-output networks in economics. 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 a given ecosystem, changes in less abundant resources or functions have the largest effects on overall ecosystem 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.

Niche Differentiation within Ecosystem Functions. A first key finding regarding the effects of species richness within functional groups is that more diverse functions have higher output, with smaller output gains from increases in the number of species at higher levels of biodiversity. In other words, the output of an ecosystem function is an increasing and concave function of biodiversity. Discussing the evidence for this relationship, which the ecology literature calls the "biodiversity-productivity relationship,"[7] 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, experimental studies found that total plant biomass on a fixed plot of land was increasing with 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, 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.*"

The observed positive relationship between species richness and function-level output is driven by "niche differentiation," which captures that different species within a function extract resources and perform services in somewhat different ways—they focus on different "niches." This feature leads to two channels through which such niche differentiation contributes to higher function-level output.

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[7] While this terminology refers to productivity—which economists often use mean output per unit of input—the ecology literature sometimes uses this term to refer to the fact that overall functional output (e.g., total biomass or biomass growth) is increasing in biodiversity. As we describe in the next paragraphs, empirical evidence shows that biodiversity can affect the overall output in a function both by increasing the total number of organisms and by increasing the output per organism.

The first channel through which niche differentiation contributes to a positive relationship between biodiversity and function-level output is by allowing more diverse functions to sustain a larger *community abundance*, that is, to support more individuals across all species in the function. 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.*" In other words, since "*each species inhibits itself more than it inhibits the other species,*" more diverse functions allow for more efficient resource extraction and thus larger community abundance (Tilman, Isbell and Cowles, 2014). For example, 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, allowing for higher abundance (Williams et al., 2017). Direct support for this "niche differentiation in resource extraction" mechanism comes from experimental work that highlights that more diverse plant ecosystems drew soil nitrate levels down to lower levels of concentration (Tilman, Isbell and Cowles, 2014).

The second channel through which niche differentiation affects overall productivity by raising functional productivity *conditional on abundance*: that is, even if the total number of individuals is the same, having different species perform the same function can yield more ecosystem services. For example, Hoehn et al. (2008) showed that when different pollinator species are active at different times of the day, or when they visit flowers of different heights, this "niche differentiation in service provision" can cause overall crop yields to rise with species diversity even holding fixed total pollinator abundance.

In addition to the biodiversity-productivity relationship, a second key finding in ecology is that the output of more diverse ecosystem functions varies less over time in response to environmental fluctuations and species loss. 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: "*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).[8]

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[8] The insight that more diverse systems are more resilient and productive—and, in fact, are more productive than the most productive monoculture (Hooper et al., 2005; Tilman, Isbell and Cowles, 2014)—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).

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. These functions include groups of species providing the same primary ecosystem services E_g, such as soil fertilization, pollination, water purification, 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.[9]

1.2.1 Imperfect Substitutability of Species Within Each Function

The species in each function interact to produce a flow of function-specific ecosystem services E_g. As discussed in the prior section, the key force driving the relation between biodiversity and functional productivity is niche differentiation, which operates through two channels: by raising community abundance and by increasing productivity for a given abundance. We model both channels in a tractable way.

Ecosystem services in function g are produced through a constant elasticity of substitution (CES) aggregator across the abundances of all species i in function g, given by $n_{i,g}$:[10]

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

Consistent with the ecological evidence, we assume that, within each function, species are highly, but not perfectly, substitutable in the production process, with elasticity of substitution ϵ_g such that:

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

In the absence of niche differentiation in service provision, species would be perfect substitutes ($\epsilon_g \to \infty$), and equation (2) would be the sum of populations across species: $E_g = \sum_{i=1}^{S_g} n_{i,g}$. In that case, two species with abundance of 50 each would have the same output as one species with abundance 100. Our modeling of a finite substitutability captures the ecological evidence that, due to niche differentiation in service provision, species are imperfect substitutes in terms of ecosystem services production: the output of two species with abundance 50 each is higher than the output of one species with abundance 100. These gains from differentiation across species are analogous to the "love of variety" effects arising from firm specialization (Dixit and Stiglitz, 1977), which play a key role in models of international trade and endogenous growth (Krugman, 1980; Romer, 1987; Matsuyama, 1995).

We next model the effect of niche differentiation in resource extraction on the relationship between

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[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.

[10] The CES functional form, assumed for tractability, implies symmetry in the interactions of species. In reality, interactions across species within a function are not symmetric (see, for example, Groom and Fontes, 2021), and a less tractable but richer model could explicitly incorporate these considerations.

biodiversity and community abundance in a function. As reviewed in Section 1.1, while different species in a function tend to compete for similar resources, niche differentiation in resource absorption suggests that the introduction of a new species will only partially crowd out existing species, allowing community abundance to increase with biodiversity. Conversely, when a species in a function goes extinct—or when it gets extirpated from the local ecosystem—resources are freed up for the remaining species, which can grow their abundances to partially compensate for the population decline from the lost species. Since this compensatory growth is weaker when species are competing less for the same resources, species loss will lead to a larger decline in community abundance in functions with more niche differentiation in resource extraction.

In principle, these dynamics could be modeled using Lotka-Volterra models, which describe full dynamic systems governing the evolution of abundances in response to changes in the number of species (Hofbauer and Sigmund, 1998). Instead of solving for the dynamic path of such models, we focus on their rest points and capture the strength of compensatory growth due to imperfect niche differentiation in resource extraction with a parameter $\alpha_g \in [0, 1]$. We denote as $\bar{S}_g > 1$ the initial number of species in functional group g, and let $s_g = S_g/\bar{S}_g$. When S_g falls below $\bar{S}_g$, surviving species in group g grow in response to the reduced competition for common resources. For simplicity, we impose symmetry among the species in a function, so that $n_{i,g} = n_g$ for each $i = 1, \ldots, S_g$.[11] We define as $\bar{n}_g$ the maximal per-species abundance that can be supported when $S_g = \bar{S}_g$. Species abundance is modeled as:

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

The equation describes how individual abundance n_g changes as S_g falls below $\bar{S}_g$. Consider two polar cases. The case $\alpha_g = 1$ implies that $n_g = \bar{n}_g$ irrespective of S_g, and therefore captures the case of "perfect" niche differentiation in resource extraction: because species were not competing for resources in the first place, removing one species does not induce compensatory growth among the remaining species.

The other polar case, $\alpha_g = 0$, implies the other species experience substantial compensatory growth when a species disappears, so much so that *total* abundance $S_g n_g$ remains at the maximum: $S_g n_g = \bar{S}_g \bar{n}_g$, because 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 compe-

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[11] When there is within-function variation in populations across species, it is more difficult to summarize biodiversity using a single number such as species richness S_g. 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" that all coincide with S_g in the symmetric case. That said, Fenichel, Dean and Schmitz (2024) correctly highlight that in the non-symmetric case, such indices are by themselves of limited use to capture the *value* of biodiversity if their parametrization (e.g., the weights assigned to each species and the order q of the Hill number) does not depend on the (endogenous) value of the species. By proposing a way to explicitly model the dependence of human welfare onto ecosystem services production and in turn onto the various species, and thereby endogenously modeling the economic value of each species, our framework can help overcome these limitations of standard measures of biodiversity. In this sense, our model answers the call from Fenichel, Dean and Schmitz (2024): "*There is a clear path forward for measuring the value of changes in biodiversity. First, recognize that biodiversity is not something that can be rolled up into an arbitrary index; rather it is shorthand for the assembly of life in a well-defined geography that accounts for ecological and human interactions. The best way to measure biodiversity is to measure the marginal value of specific species, or groups of species belonging to a community, and condition valuation on ecological interactions and interactions with people. Measured species can be added to balance sheets as nonfinancial, nonproduced assets. Then changes in biodiversity are changes in the wealth contribution of those species.*"

tition 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. This would represent the case of no niche differentiation in resource extraction.

In practice, values of α_g between 0 and 1 are most consistent with the empirical evidence for partial niche differentiation in resource extraction discussed in Section 1.1. Plugging n_g in equation (3) into the within-function aggregator given by equation (2), ecosystem services from function g equal:

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

The variables α_g and ϵ_g thus allow for separate parameterizations of the two forces through which niche differentiation drives a positive relationship between species richness and E_g: (i) the ability to sustain a more abundant community, with larger effects when there is less competition for common resources (high α_g); 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 in their productive activities (low ϵ_g). Ultimately, 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:

$$\phi_g = \frac{1}{\epsilon_g - 1} + \alpha_g > 0, \tag{6}$$

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 ($s_g = 1$).

To capture not just the positive nature of the biodiversity-productivity relationship ($\phi > 0$), but also its empirically-established concavity (see Liang et al., 2016, and the other references in Section 1.1), we impose $\phi_g < 1$.[12] This limits the strength of the total niche differentiation effects through the two channels—resource extraction and service provision—since stronger niche differentiation effects would push ϵ_g down while pushing α_g up, both of which would contribute towards a larger ϕ_g.[13] 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). As discussed above, lower values of ϕ_g imply more concavity in the relation between ecosystem services and biodiversity.

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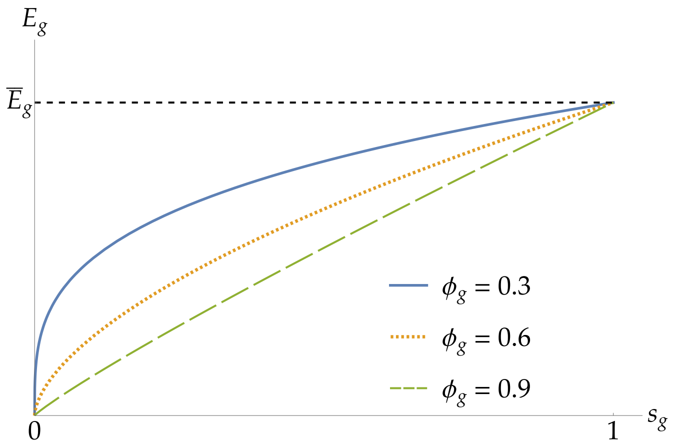
[12] The concavity of E_g with respect to s_g is also consistent with the previously discussed evidence for a positive biodiversity-stability relationship within a function. Specifically, while often treated as separate observations, the concave biodiversity-productivity relationship immediately delivers the biodiversity-stability relationship: when a function is at the species-rich flat part where additional diversity has only small positive effects on output, the loss of a particular species has equivalently small negative effects on output, and so functional output is more stable in response to external disturbances.

[13] In principle, extreme niche differentiation could even lead to a convex relationship between biodiversity and productivity. Take the case of extreme niche differentiation in resource extraction ($\alpha_g = 1$), when total abundance increases linearly in the number of species, because there is no crowding out due to competition for common resources. In that case, any small effects of biodiversity on functional productivity conditional on abundance—any niche differentiation in service provision— will lead to an overall convex relationship. While many of our empirical results only rely on a positive biodiversity-productivity relationship, whether convex or concave, the strong empirical support for a concave relationship motivates our choice to focus our analysis on the empirically relevant case $\phi_g < 1$.

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, relative to its maximum value $\bar{E}_g$ (which also varies with 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:[14]

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

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 $\sigma < 1$.[15] 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 C.2 for details on this calculation).

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[14] While it would 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 depend on the health of each function—in a tractable way.

[15] 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.3, 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 by the expected distinctiveness of their genetic content and a reduced-form "utility value" exogenously associated to each species (closely related to Weitzman, 1992; Polasky, Solow and Broadus, 1993), our ecologically-founded framework explicitly focuses on species' heterogeneous contributions to ecosystem services, and derives their value endogenously, consistent with arguments in Brock and Xepapadeas (2003) 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:

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

which is increasing in each S_g, with marginal effects given by:

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

Proposition 1 further characterizes this marginal effect of species loss on aggregate ecosystem services, taking into account that E and E_g in equation (9) also depend on S_g. As described previously, we continue to assume that $\sigma < 1$ and $\phi_g < 1$.

Proposition 1. *The marginal effect of a species shock dS_g on ecosystem service production is decreasing in S_g, so that aggregate ecosystem service provision E is concave in S_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., $S_g \to \infty$.

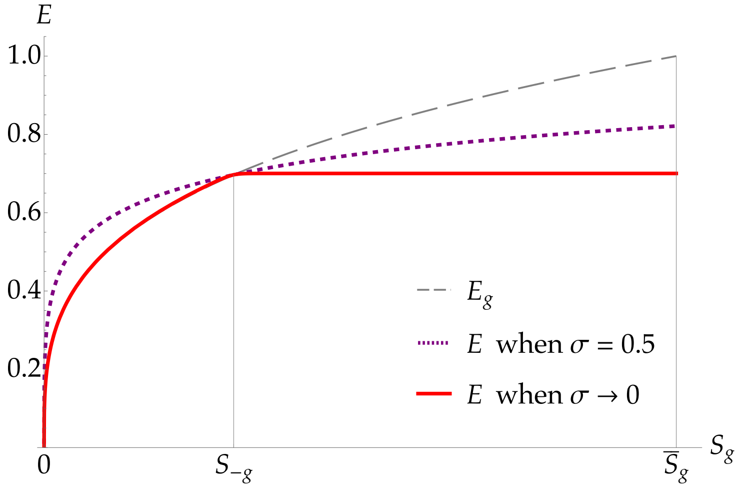
Critical Functions. *The effect of a species shock dS_g becomes infinitely large as $s_g = S_g / \bar{S}_g \to 0$:*

$$\lim_{s_g \to 0} \frac{\partial E}{\partial S_g} = \infty. \tag{10}$$

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. The effect of species loss in a function on ecosystem output becomes more negative at lower levels of biodiversity both because the marginal effects of S_g on E_g get bigger, and because E_g becomes more constraining for overall ecosystem output. Conversely, 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 total ecosystem service production.

Figure 3 shows an example of the function-level concavity (gray dashed line, similar to Figure 2 with $\phi_g = 0.3$) as well as the additional concavity in the relationship between aggregate ecosystem services E and S_g (dotted and solid lines, corresponding to different values for σ). In this example, the original number of species in all functions is $\bar{S} = 100$, but all functions other than g have already suffered species loss, bringing S_{-g} to 30 (where S_{-g} refers to all $j \neq g$). Even after species loss in function g has started to reduce E_g, this only affects overall ecosystem productivity E to the extent function g limits 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 the solid 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 $S_{-g} = 30$.

Figure 3: Ecosystem Service Production and Biodiversity



Note: Figure shows E_g as functions of S_g, as well as E as a function of S_g for two values of σ, with $\phi_g = 0.3$, $S_{-g} = 30$, normalizing $E = 1$ when $S_g = S_{-g} = \bar{S} = 100$.

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 can hide an increasing exposure to further losses. Indeed, Figure 3 shows that our ecologically-founded modeling approach generates the presence of nonlinearities in the relationship between biodiversity and ecosystem service production. The absence of such nonlinearities from existing models has been lamented by researchers studying the economic effects of biodiversity loss (e.g., Svartzman et al., 2021); the need to explicitly model these nonlinearities when valuing biodiversity has also been recently highlighted by Fenichel, Dean and Schmitz (2024).[16]

A second implication of the concavity of E with respect to S_g is that 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 aggregate ecosystem services.[17] This conclusion is consistent with empirical evidence that past losses of keystone species have had meaningful ecological and economic effects (see Appendix A). For example, Frank and Sudarshan (2024) find large costs from the collapse of the vulture population in India, which led, among other things, to a 4% increase in human mortality due to a decline in sanitation services. The authors emphasize that vultures were without a "*good functional replacement in the ecosystem.*"

More generally, 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 (MRS):

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

The MRS between different species helps 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,*" are a key component of environmental regulation in many jurisdictions, including in Great Britain, the European Union, and the United States. One principle of biodiversity offsets is that they should lead to a "no net loss" outcome (McKenney and Kiesecker, 2010; Aronoff and Rafey, 2023). Our findings highlight the importance of specifying the exact metric for "no net loss" given that "no net loss of species" does not generally translate into "no net loss for ecosystem functioning." The MRS between species can also help impact investors choose between sustainability-linked bonds that link coupon payments to the achievement of various biodiversity objectives, such as Klabin's $500m bond for which payments depend on the successful reintroduction of extinct species into ecosystems (Aleszczyk, Loumioti and Serafeim, 2022).

2.2 Biodiversity Shocks and the Fragility of Ecosystem Services

Proposition 1 above highlights the highly non-linear effects 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

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[16] The nonlinearity stemming from this concavity helps us describe situations where the effects of biodiversity loss progressively worsen as the ecosystem experiences a sequence of stressors or shocks. This type of nonlinearity is conceptually different from the notion of "tipping points" due to non-convexities or discontinuities described in Brock and Starrett (2003), de Zeeuw (2014), and Li, Crépin and Lindahl (2024). Our model could potentially be extended to account for tipping points by modeling population dynamics as reviewed in, e.g., Li, Crépin and Lindahl (2024).

[17] Our framework can also accommodate slightly different notions of keystone species, for instance species that contribute to several ecosystem functions, or species that form their own ecosystem function with an especially low elasticity of substitution with other functions.

how the aggregate impact of an arbitrary distribution of species losses across multiple functions depends on the current state of biodiversity captured by the vector $\boldsymbol{s} = \{s_g\}_{g=1,\ldots,G}$. Throughout this section, we simplify expressions by assuming that $\bar{n}_g$ and $\bar{S}_g$ are the same across all functions.

We consider a loss of biodiversity in several functions, given by the vector $\boldsymbol{ds} = \{ds_g\}_g$; in the Appendix, we extend this result to additionally allow for shocks to species abundances holding the number of species fixed. We consider the impact of additive species shocks ds_g (and not, say, multiplicative shocks $d\log s_g$), 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). Proposition 2 decomposes the effect of such an additive shock to biodiversity $\boldsymbol{ds}$ into three conceptually distinct parts.

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

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

where we denote:

$$\omega_g = \frac{N_g}{\sum_{j=1}^{G} N_j} \qquad \textit{(abundance weights)},$$

$$\mu_g = \frac{\partial \log E}{\partial \log E_g} = \frac{s_g^{\phi_g \frac{\sigma-1}{\sigma}}}{\sum_{j=1}^{G} s_j^{\phi_j \frac{\sigma-1}{\sigma}}} \qquad \textit{(criticality weights)},$$

$$\gamma_g = \mu_g - \omega_g \qquad \textit{(criticality-abundance gap)}.$$

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

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

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

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

Before providing intuition for Proposition 2, 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 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.[18] In the Cobb-Douglas limit $\sigma \to 1$, all the μ_g would be equal to $1/N$, just like factor shares are constant with Cobb-Douglas production functions. With σ strictly below 1, as we assume, the 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 higher ϕ is more critical. Higher complementarity across functions (lower σ) also magnifies differences in criticality due to variations in biodiversity s_g.

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 function g contributes more productively to aggregate ecosystem services at the margin than its population share. A positive gap can happen, for example, if 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, with a lower σ amplifying the absolute magnitudes 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 first channel comes from a fall 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 magnitude of the community-abundance effect depends on the extent of compensatory growth of remaining species. The more intense the within-function competition for resources (lower α_g), the more the extinction of some species benefits the surviving ones. In the extreme case of no niche differentiation in resource absorption and thus full compensatory growth ($\alpha_g = 0$), community abundance is unaffected by species loss. Crucially, this first effect would operate even if all species across all functions were perfectly substitutable at performing ecosystem services (i.e., if $\epsilon_g = \sigma = \infty$).[19]

The second term, $\sum_{g=1}^{G} {}^{\omega_g}/_{s_g(\epsilon_g - 1)} ds_g$, captures that due to niche differentiation in service provision, functional groups with fewer species have lower output E_g, even holding community abundance in the function fixed. When biodiversity in a function has been depleted more (low s_g), further biodiversity losses in that function have larger negative effects on the productivity of the function and therefore lead to bigger losses in aggregate ecosystem service provision. These effects are stronger in functions with less substitutability across species (low ϵ_g, corresponding to more niche differentiation in service provision) and disappear if $\epsilon_g \to \infty$ for all g, that is, if species in a function are perfect substitutes.

The final term, $\mathrm{Cov}\left[\gamma_g, {}^{\phi_g}/_{s_g} ds_g\right]$, 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 species across functions ($s_g = s$), in which case $\gamma_g = 0$. If instead there are pre-existing imbalances in s_g, the covariance term can be non-zero.

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[18] 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 ${}^{wL}/_{Y} = {}^{\partial \log Y}/_{\partial \log L}$, and factor shares sum to 1 when Y is homogeneous of degree 1 as in the CES case.

[19] 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.

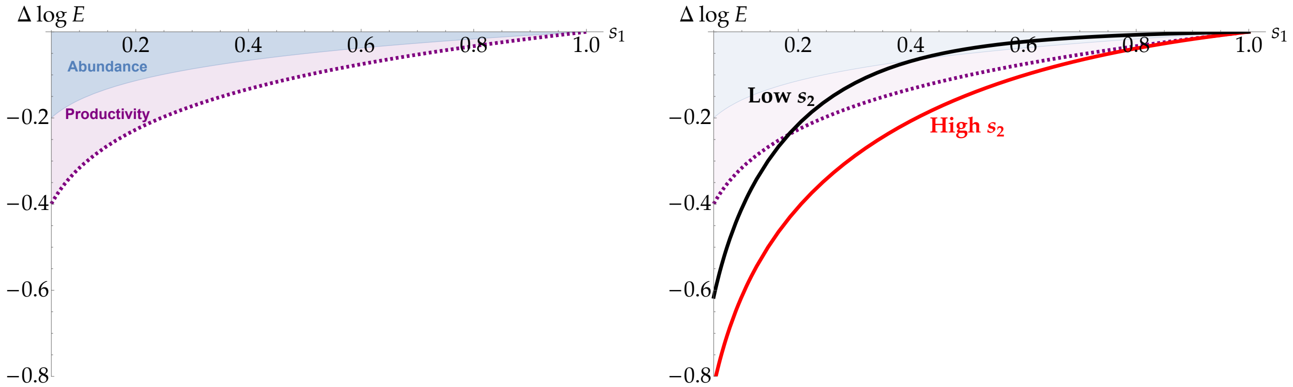
This last term is reminiscent of the literature on the aggregate implications of misallocation of inputs across firms and sectors. While the underlying nested-CES framework relates to models of the economy that consider firms and industries—and we can therefore apply some of the insights from the seminal work of, e.g., Hsieh and Klenow (2009), Baqaee and Farhi (2019*a*,*b*)—the 'shocks' we consider in our setting are fundamentally different, as species loss (which could be induced by land-use, as in Section 4) directly affects the mass of species and the abundance of surviving species via compensatory growth effects. Another important distinction between firms and species is that unlike firms' production choices, species loss is not the outcome of multiple profit-maximization problems coordinated by a price system. The initial allocation of species can therefore be highly 'inefficient,' in the sense that E might be increased by 'reallocating' species from less critical functions to more critical ones. As a result, the change in imbalances appears as a *first-order* effect as in Baqaee and Farhi (2019*b*) and Bigio and La'O (2020), which contrasts with the case of 'efficient' production networks, in which Hulten's theorem applies and changes in allocative efficiency are only relevant at the second order (Baqaee and Farhi, 2019*a*). New biodiversity losses have stronger effects when they disproportionately hit functions with a higher abundance-criticality gap ($\text{Cov}\left[\gamma_g, {}^{\phi_g}/_{s_g} ds_g\right] < 0$), and smaller effects 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 the latter case of a positive $\text{Cov}\left[\gamma_g, {}^{\phi_g}/_{s_g} ds_g\right]$, the net effect of species losses on aggregate ecosystem production is still weakly negative when summing up the three terms in equation (12); however, a simple abundance-based measure that considers only the first term—or even a more sophisticated measure that also accounts for additional niche differentiation effects in the performance of ecosystem services captured by the second term—would overestimate the reduction in ecosystem services.

Once again, the intuition for the across-function effects driving the third term is clearest in the limit of no substitution between functions ($\sigma \to 0$). In that case, if 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 function-level productivity conditional on abundance. In that case, the third term in our decomposition in equation (12) is positive and exactly offsets the first two negative terms capturing abundance loss and decreased niche differentiation in the performance of ecosystem services (also see Figure 3). More generally, the covariance term $\text{Cov}\left[\gamma_g, {}^{\phi_g}/_{s_g} ds_g\right]$ 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 graphical intuition for 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 fixed. Panel A shows the cumulative reduction in ecosystem services relative to the initial condition $s_1 = 1$ due to the first two terms in equation (12), that is, ignoring any effect of cross-functional imbalances (e.g., if all ecosystem functions were perfectly substitutable, $\sigma \to \infty$). The blue region labeled "Abundance" captures the reduction in ecosystem services due to the effect of lower community abundance. The purple region labeled "Productivity" captures the additional productivity loss due to decreased niche differentiation in the performance of the ecosystem function.

Panel B shows the cumulative reduction in ecosystem services taking into account all three channels in equation (12). We hold the abundance and productivity effects fixed, hence the dotted purple line is

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 community abundance and the purple region ("Productivity") to the second term due to changes in function-level productivity conditional on abundance. 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 of 0.4, and the solid red line ("High s_2") holds s_2 fixed at 1. In 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., $\epsilon_g \approx 7.7$).

the same as in Panel A. We highlight the role of cross-functional imbalances by showing how E declines under two scenarios: one where 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 absolute 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 within-function niche differentiation effects on abundance and productivity. In the Figure, the gap between the solid red line and the dotted purple line captures the cumulative third term in equation (12) due to increased imbalances between functions as more species are lost in function $g = 1$.

When s_2 is low, 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 $g = 1$, depicted by the solid black line, is much smaller than implied by within-function niche differentiation effects: while species loss reduces the abundance and productivity 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- and productivity-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 loss in function 1 is so large that function $g = 1$ becomes depleted relative to the other functions, the black line crosses the dotted purple 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 within-function loss in abundance and productivity, as in the "High s_2" case.

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 across ecosystem functions. 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 in the performance of ecosystem services and let $\epsilon_g \to \infty$, which drops the second of the three terms in equation (12). Then fragility can be expressed as:

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

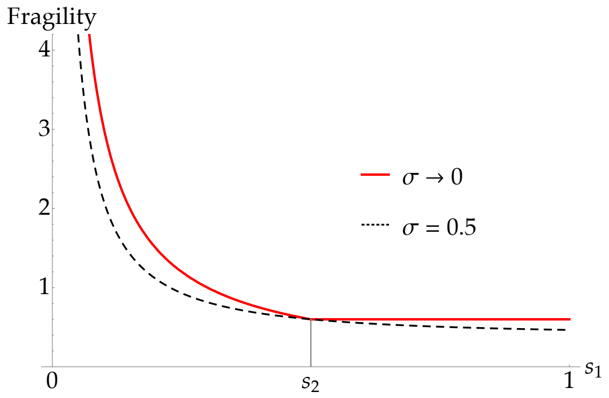
Both terms are always positive, with the second term equal to zero if and only if initial conditions are symmetric, $s_1 = s_2$: imbalances always increase ecosystem fragility and thus add to overall loss of ecosystem services in response to a common shock (this contrasts with the case of asymmetric species loss which might "even things out" by disproportionately hurting 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 still 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 from further species losses—varies. In Appendix C.4, 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, if species loss over time tends to cluster in a subset of functions, this leads to additional increases in fragility over time.

Fragility of Ecosystem Services: Approximation. To allow us to eventually measure the fragility of different ecosystems—something we attempt to do below—we also derive a first-order approximation to express fragility as a function of two ecosystem properties that can be observed in the data (see Ap-

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 correspond to different values of σ.

pendix C.9 for details on the approximation): the *average* and *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:

$$\mathcal{F}(\boldsymbol{s}) \approx \frac{\phi}{\bar{s}} \times \left\{1 + \left[1 - \phi + \frac{\phi}{\sigma}\right] \mathrm{Var}(\delta_g)\right\}, \tag{14}$$

where $\mathrm{Var}(\delta_g) = \sum_g \delta_g^2$. The term $\phi/\bar{s}$ is the only source of fragility if losses are symmetric across 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 across functions captured by $\mathrm{Var}(\delta_g)$ increases fragility. Dispersion has a stronger impact if σ is lower, that is, if different ecosystem functions are less substitutable.

3 Biodiversity Loss, Fragility, and Economic Activity

The theory developed so far has modeled the dependence of ecosystem services on biodiversity. We now embed this representation into the aggregate production function, the next step to obtaining an integrated model of the economy and nature. From this representation, we derive testable predictions that link an economy's exposure to biodiversity loss—summarized by the concept of ecosystem fragility—to its economic consequences, and show how these predictions can be evaluated in the data. In Section 4, we then build on this integrated model to study optimal policy.

3.1 Integrating Biodiversity into Economic Production

For now, we focus on capital K as the only factor of production beyond ecosystem services. We denote total factor productivity (TFP) as A, and write equation (1) as:

$$Y = A\, F(K, E(\boldsymbol{s})) \tag{15}$$

where the term $E(\boldsymbol{s})$ reflects the dependence of ecosystem services on biodiversity $\boldsymbol{s}$.

For many of the results derived in this paper, the exact functional form of F is not essential: often, the results depend only on the elasticities of output to capital and ecosystem services, $\eta^K = \partial \log F / \partial \log K$ and $\eta^E = \partial \log F / \partial \log E$, which, for our purposes, can be left unspecified. In some cases, however, it is useful to pick a specific analytical form for F. A useful one is the standard CES function, which could of course be expanded to include additional factors of production such as land and labor:

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

The advantage of this functional form is that it allows us to study how economic outcomes vary with the degree of substitutability or complementarity between ecosystem services and capital, captured by ξ. The ease with which capital can replace ecosystem services is central to valuing nature's role in production: intuitively, conservation becomes more important the harder and costlier it is to substitute capital for the economic functions provided by nature. A long literature including Pearce and Atkinson (1993), Ekins et al. (2003), Dietz and Neumayer (2007), and Ayres (2007) has empirically investigated whether ξ is above or below one. Researchers typically distinguish between the "strong sustainability" hypothesis ($\xi < 1$, limited substitutability between capital and nature) and the "weak sustainability" hypothesis ($\xi > 1$, greater substitutability). The strong sustainability view was central 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*." In what follows, unless otherwise specified, we remain agnostic about whether ξ is above or below one, since our qualitative results do not hinge on this distinction (though the quantitative implications of a calibrated model would).

3.2 Testable model predictions

The theory developed so far links biodiversity $\boldsymbol{s}$, ecosystem services $E(\boldsymbol{s})$, and output $F(K, E(\boldsymbol{s}))$. In this section, we derive testable implications of the model and take them to the data. To begin, we return to the general specification in equation (15), specializing it to countries ℓ:

$$Y_\ell = A_\ell F_\ell(K_\ell, E(\boldsymbol{s}\ell)). \tag{17}$$

This specification implies that biodiversity loss in country ℓ reduces output Y_ℓ. Yet, as previously discussed, the direct effect of ecosystem damage on economic activity may take time to materialize, making it difficult to directly link the two. Moreover, biodiversity loss can increase ecosystem fragility well before measurable economic damages occur. For this reason, we focus on model implications that relate countries' *exposure* to biodiversity loss to the *risks* facing future economic activity—two quantities that, as we argue below, can be measured in the data.

Specifically, we assume that country ℓ defaults on its outstanding government debt if output falls sufficiently. In our model with capital and nature, this output loss can be due to a combination of a negative TFP shock and/or a species loss shock ds_ℓ. The probability of default can be written as:

$$\mathbf{Pr}\left[d \log Y_\ell \leq z_\ell\right] = \mathbf{Pr}\left[\eta_\ell^E \mathcal{F}(\boldsymbol{s}_\ell) ds_\ell + d \log A_\ell \leq z_\ell\right], \tag{18}$$

where the default threshold z_ℓ depends on country characteristics such as the level of government debt, tax rates, and interest rates. As before, $\eta_\ell^E = \frac{\partial \log F_\ell}{\partial \log E_\ell}$ denotes the elasticity of output to ecosystem services.

Suppose that each country faces log-normal TFP shocks, $d \log A_\ell \sim N(\mu, \sigma^2)$, as well as independent species loss shocks distributed according to an exponential distribution with rate $1/\theta$. The expected species loss is thus $ds_\ell = -\theta$. We can then ask the following question: what happens when there is an exogenous increase in the probability of biodiversity loss? In this framework, such negative news about biodiversity risk would correspond to an increase in the parameter θ indexing the distribution of species loss shocks. Then, to first-order in fragility $\mathcal{F}(\boldsymbol{s}_\ell)$, we have

$$\mathbf{Pr}\left[d \log Y_\ell \leq z_\ell\right] \approx \Phi\left(\frac{z_\ell - \mu}{\sigma}\right) + \theta\, \eta_\ell^E\, \mathcal{F}(\boldsymbol{s}_\ell)\, \sigma^{-1} \phi\left(\frac{z_\ell - \mu}{\sigma}\right), \tag{19}$$

where Φ and ϕ are the c.d.f. and p.d.f. of a standard normal distribution, respectively. A key prediction is that a negative biodiversity news shock will increase the overall country default probability by an amount that is proportional to the ecosystem fragility of that country. Equation (19) therefore links news about biodiversity loss (θ) to default risk (the left-hand side probability) via biodiversity exposure (the fragility term).[20] It also shows that even an increase in mean species loss that is common across countries will generally lead to heterogeneous effects across countries: credit risk responds more strongly to negative biodiversity news in countries with higher fragility $\mathcal{F}(\boldsymbol{s}_\ell)$ or higher importance of ecosystem services in production η_ℓ^E. In the next section, we empirically explore this cross-country link between country default risk, news about biodiversity loss, and the two main components of fragility: average biodiversity degradation and dispersion across functions, as highlighted in equation (14).

3.3 Biodiversity Loss, Fragility, and Economic Activity: Empirical Evidence

There are many well-identified cases studies documenting how biodiversity loss can having meaningful negative economic effects, especially when the losses affected functions with little functional redundancy (e.g., Frank, 2024; Frank et al., 2024); we describe several of these studies in detail in Appendix A. There, we also review the economic implications from past instances of local ecosystem collapse, including the collapse of the Aral Sea ecosystem, and the ecosystem collapses associated with both the American Dust Bowl in the 20th century as well as the present-day Chinese Dust Bowl. While these case studies exemplify the potential economic consequences of biodiversity loss, in this section we present a more systematic empirical assessment of some of the key implications of the model that relate biodiversity loss and ecosystem fragility to economic risk (see Section 3.2).

In particular, we argue that *asset prices* provide invaluable inputs in testing these relationships. Focusing on asset prices rather than measures of economic output has two advantages. First, asset prices are forward-looking, and reflect expectations about long-term cash flows and risks—even those that have not yet affected current economic activity. Second, while economic activity and biodiversity loss move slowly, news about (and attention to) current and future biodiversity loss can vary more more

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[20] Above, we illustrated this point using specific shock distributions. More generally, if TFP shocks $d \log A_\ell$ are distributed according to a c.d.f. G_A, and independent species loss shocks ds_ℓ are distributed according to a c.d.f. $G_s(\cdot|\theta)$ that depends on a parameter θ, then the default probability is $\mathbf{Pr}\left[d \log Y_\ell \leq z_\ell | \theta\right] \approx G_A(z_\ell) + \eta_\ell^E \mathcal{F}(\boldsymbol{s}_\ell) G_A'(z_\ell) \mathbf{E}[-ds_\ell|\theta]$. The first term is the baseline default probability absent nature shocks. The second term is the increase in default risk due to nature shocks.

frequently, and asset prices should reflect such changes immediately. As a result, researchers have more empirical variation to detect possible relationships in the data.

At a high level, our test of the model proceeds as follow. First, we use asset prices to obtain a high-frequency measure of forward-looking economic risks at the country level. Specifically, we measure country-level risk by studying sovereign credit default swaps (CDS), which are financial contracts with a payoff that depends on an underlying country defaulting on its debt obligation.[21] The prices of CDS (referred to as "spreads") reflect the evolution of the country's expected default probability, corresponding to the left hand side of equation (19). We also measure high-frequency negative news about biodiversity loss from newspapers, which can be interpreted as reflecting shocks to θ. Finally, using disaggregated data on species loss, we measure the two main components of fragility at the country level: the average biodiversity loss and the dispersion in biodiversity loss across functions. We then use the objects to test the economic mechanism of equation (19): bad news about biodiversity loss should lead to increases in country risks 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 specifically predicts that news about biodiversity losses should increase economic risks more for countries with biodiversity that is more degraded on average (Proposition 1) and more for countries where the degradation of biodiversity is more uneven across ecosystem functions (Proposition 2).

3.3.1 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 and EUR-denominated CDS. 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; we use the "par spread" measure throughout our analysis). After merging this CDS data with the measures of biodiversity loss described below, we obtain a sample of about 865,169 weekly changes in CDS spreads for 99 distinct countries between 2001 and 2023 (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 (instead of studying absolute changes). At the 5th percentile of the distribution, CDS spreads fell by 12.4 percent in a week; at the 95th percentile, they increased by 15.3 percent. The 5-year tenor is the most common at 18.8% of the sample, while long maturities of 30 years are the least common at 14.9% of the sample.

Negative Biodiversity News. To measure aggregate news about biodiversity loss, as well as attention to such loss, we build on the empirical work of Giglio et al. (2023), who produce a daily index of news coverage of biodiversity loss in the *New York Times*. Appendix Figure B.1 shows a monthly version of this index to illustrate broader trends, with positive values corresponding to periods with more bad news

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[21] Alternatively, one could study different countries' yields spreads (obtained from the prices of their government bonds). In practice, CDS spreads and bond yields spreads are tightly related via a no-arbitrage condition, so that, barring liquidity-related frictions, they contain the same information. CDS spreads, however, tend to be more liquid and standardized, making them better suited for studying credit risk (Longstaff, Mithal and Neis, 2005). One could also study equity markets (e.g., via indices like the S&P 500 for the U.S.), but the breadth and liquidity of equity markets is significantly smaller in developing countries, making them much less informative about the country's economic prospects than in developed markets. In contrast, CDS spreads for *all* countries are usually traded and cleared in clearinghouses in the U.S., Europe, and Japan.

about biodiversity loss (corresponding to increases in θ in equation 19). To isolate the unanticipated component of negative biodiversity news, we aggregate this index to the weekly level and construct AR(1) residuals, similar to the approach in Engle et al. (2020) and Alekseev et al. (2025).

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 B 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.[22]

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 use this value as of 2012, which aligns roughly with the mid-point of our CDS data series, though we show robustness of the results to using the 2022 data and the average across measures at both points in time. Appendix Table A.1 shows the *BiodiversityDestructionScore* by country in 2012, 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; this 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. Countries with the highest scores (corresponding to the most biodiversity destruction) span a wide geographic range, with Uruguay, Portugal, Panama, Trinidad and Tobago, and Indonesia ranking at the top. 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. Measuring the dispersion of species loss across ecosystem functions—the second key object driving ecosystem fragility—requires combining several data sets.

To measure the population health of different species, we work with the *Map of Life* database introduced by 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 B for details). These area scores measure a species' habitat-suitable range in the country as a percentage of that range in 2001, and serve as good proxies for changes in species abundance, since habitat loss generally reduces species abundance and increases extinction risk (Newbold et al., 2015;

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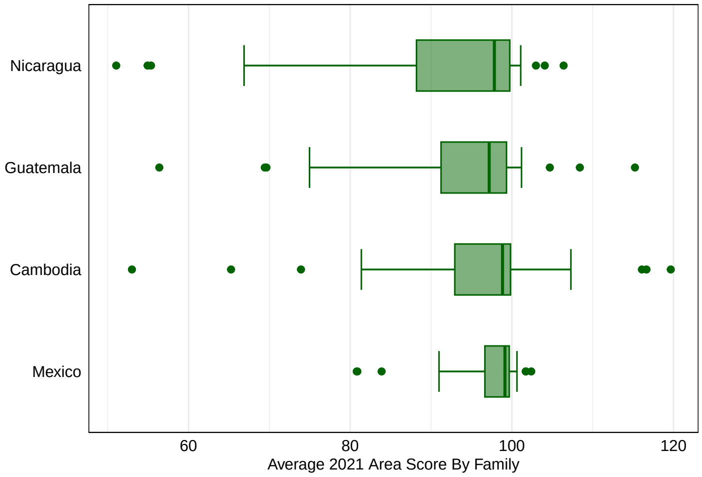
[22] We prefer the *BiodiversityDestructionScore* to the average habitat loss from the Map of Life data described below as our baseline measure of average biodiversity loss in a country. This is because the EPI data incorporates many more species and ecosystems than the Map of Life data, which only includes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

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



Note: Figure shows a 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 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.

Powers and Jetz, 2019; Andre, Groom and Venmans, 2025). 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 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 population health proxies and functional classifications for over 2 million species-country-years covering 221 countries and territories. In 2012, 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 of an average species family in 2021 was only 2–4% smaller than in 2001, while in Guatemala and Nicaragua the average family had lost 6–8% of its range. Even among countries with similar average loss, the variation across families differs widely: at the 10th percentile, family-level ranges had declined by 26% in Nicaragua compared to 18% in Guatemala. One Nicaraguan family that has suffered particularly severe habitat loss is the *Atelidae*, whose range shrank by 36% between 2001 and 2021. This family includes the endangered Nicaraguan Spider Monkey, whose decline—driven largely by habitat loss (Cortes-Ortìz et al., 2020)—threatens seed dispersal processes essential for plant population dynamics and ecosystem health. Conversely, conservation programs such as reforestation along the Pacific Slope have expanded the *Felidae* family's habitat by 0.9%, supporting species like the Ocelot.

Similarly, while Cambodia and Mexico experienced comparable overall habitat loss, Cambodia shows much greater variation across families. At the 10th percentile, family-level habitat declined by 13% in Cambodia versus 6% in Mexico. One Cambodian family with especially severe losses is the *Hylobatidae*, whose habitat contracted by 35% between 2001 and 2021. This family includes the Northern Yellow-Cheeked Gibbon, endangered largely due to this loss (IUCN, 2020). Like the Atelidae, they play a crucial role in seed dispersal, and their decline undermines forest stability. In contrast, targeted efforts for the near-extinct Hog Deer have increased the *Cervidae* family's habitat by 8%.

We obtain our $AcrossSuborderHabitatLossDispersion$ measure by taking the standard deviation of the average habitat loss across families in a country. In our baseline analysis, we focus on the dispersion in the year 2012, which is approximately in the middle of the our CDS sample, and aligned with the time at which we measure the $BiodiversityDestructionScore$. Appendix Table A.3 shows the across-family dispersion of habitat destruction by country in 2012.

3.3.2 Empirical Analysis

Empirical 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 regression:

$$\begin{aligned}\Delta CDS\_Spread_{i,m,c,t} = \alpha &+ \beta_1 BiodiversityNews_t \\ &+ \beta_2 BiodiversityNews_t \times BiodiversityDestructionScore_i \\ &+ \beta_3 BiodiversityNews_t \times AcrossSuborderHabitatLossDispersion_i \\ &+ \xi_{i,m,c,year} + \epsilon_{i,m,c,t}.\end{aligned} \tag{20}$$

$\Delta CDS\_Spread_{i,m,c,t}$ is the percentage change in the CDS spread for country i, at maturity m, in currency c, in week t. We winsorize $\Delta CDS\_Spread_{i,m,c,t}$ 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 more bad news (or more attention to bad news). We standardize $BiodiversityNews_t$ to have mean 0 and standard deviation 1 over the sample weeks. The variables $BiodiversityDestructionScore$ and $AcrossSuborderHabitatLossDispersion$ are also standardized to have mean 0 and standard deviation 1 across countries in our sample, which facilitates comparisons of effect sizes across regressors.[23] In our baseline regression, we include country × year × maturity × currency fixed effects. We also double cluster standard errors by month and country to account for the fact that all CDS for a given country over time and all CDS in a given month across countries might be affected by common factors.

Results. Table 1 presents estimates of regression (20). In column 1, we only include the biodiversity news index as a regressor. 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 0.20 percent, but this estimate of the average effect is not statistically significant. The lack of statistical significance and the modest size of

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[23] 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.

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 in our sample.

Table 1: CDS Spreads and Biodiversity News

	(1)	(2)	(3)	(4)	(5)	(6)
Biodiversity News	0.195	0.189	0.189	0.190	0.192	0.188
	(0.140)	(0.138)	(0.138)	(0.138)	(0.140)	(0.141)
Biodiversity News × Measure of Mean Biodiversity Destruction		0.072^{**}	0.072^{**}	0.068^{**}	0.043^{***}	0.069^{***}
		(0.029)	(0.028)	(0.027)	(0.016)	(0.023)
Biodiversity News × Dispersion of Biodiversity Losses Across Taxonomic Groups		0.052^{**}	0.040^{**}	0.050^{**}	0.053^{***}	0.047^{***}
		(0.020)	(0.018)	(0.021)	(0.016)	(0.015)
Country × Year × Tenor × Currency FE	x	x	x	x	x	x
Taxonomic Group for Dispersion Measure		Suborder	Order	Family	Suborder	Suborder
Biodiversity Destruction Measure		EPI	EPI	EPI	EPI No ESS	EVI
Observations	865,169	865,169	865,169	865,169	865,169	846,805

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 at the 1% level. All regressions include country-year-tenor-currency fixed effects. Column 2 adds interactions of innovations in biodiversity news and our baseline measures: the *Biodiversity Destruction Score*, an aggregate measure of physical indicators of biodiversity destruction in 2012; and the *Across Suborder Habitat Loss Dispersion*, the standard deviation of area scores across suborders of within-suborder average area scores in 2012. Columns 3 and 4 replace the across-suborder dispersion with the standard deviation of area scores across orders and across families, respectively. Columns 5 and 6 replace the aggregate measure of physical indicators with two alternative measures: an version of the EPI that excludes fisheries and Ecosystem Services (ESS), and 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 mean and dispersion of biodiversity degradation. Standard errors are in parentheses and are double clustered at both the country and at the month levels. Significance levels: * ($p<0.10$), ** ($p<0.05$), *** ($p<0.01$).

Column 2 introduces interactions between biodiversity news and two determinants of countries' biodiversity risk exposures: the biodiversity destruction score and the across-suborder dispersion of habitat destruction in 2012. The estimated coefficient on the interaction with the biodiversity destruction score, β_2, suggests that CDS spreads are 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 0.072 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 212 basis points, this corresponds to a very modest differential increase in CDS spreads of about 1 basis point.

The estimated coefficient on the interaction with across-suborder 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, holding the average destruction fixed. This suggests that habitat destruction that is more concentrated in a few functions increases ecosystem fragility, consistent with Proposition 2. A one standard deviation increase in habitat destruction dispersion raises the effect of negative biodiversity news on CDS spread changes by 0.052 percentage points.

Columns 3 and 4 replace $AcrossSuborderHabitatLossDispersion$ with measures of the across-order and across-family dispersion of habitat destruction, respectively. The results are robust to these alternative measures of the dispersion of biodiversity losses across taxonomic groups. Column 5 replaces *BiodiversityDestructionScore* with a version of the EPI that excludes ecosystem services and fisheries. Column 6 instead uses the Environmental Vulnerability Index (EVI), which assesses a country's vulnerability to environmental hazards (see Kaly, Pratt and Mitchell, 2004). Estimates are similar with these alternative measures of average biodiversity loss, both of which are further described in Appendix B.

Robustness. In Appendix B, we show that our results are robust to adjustments in the data construction choices. For example, we use several alternative measures of across-suborder imbalances in biodiversity: using the 10th percentile or the minimum value of area scores across suborders, and using 2021 values for our dispersion measure instead of 2012 values. The results are similar regardless of the measure of imbalance in habitat loss. Similarly, we show that the results are robust to using alternative periods for mean biodiversity destruction. Finally, we show that the results are unchanged when we apply a different winsorization threshold and when we restrict our sample to USD-denominated CDS only.

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 higher ecosystem fragility. While the magnitudes of the effect sizes are small, the evidence suggests that our ecologically founded measures of ecosystem fragility capture key aspects of the ways in which biodiversity loss affects economic risk. It is important to note that these findings need not imply that analysts trading CDS explicitly consider our two exposure indicators. Instead, the observed relationships more likely result from the fact that in countries with larger and more dispersed past losses of biodiversity, those past biodiversity losses are already putting substantial strain on ecosystem services production and thus economic output. To the extent that such economic losses are already more salient in those countries, analysts focusing on these countries would naturally pay more attention to news about biodiversity loss.

Consider Malaysia, the country with the fifth-highest across-family dispersion of biodiversity losses. A recent World Bank and Bank Negara Malaysia (2022) report highlights that "*high levels of economic growth in the last two decades [...] have 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*" and concludes that there are meaningful economic risks from such losses. 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 second-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, 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. Allianz (2023) estimates the loss of pollination services in Portugal will result in a 6.5% decrease in agricultural output and a reduction of the country's GDP by about 0.4%.

In other words, in countries like Portugal and Malaysia, where biodiversity degradation already disrupts key industries, the economic effects of biodiversity loss are already meaningful. This makes biodiversity risk more salient to the analysts tracking these countries, and increases the probability that they will incorporate biodiversity-related risks in their financial assessments.

4 Optimal Conservation Policies

The final section examines the economic rationale for biodiversity conservation, focusing on the optimal allocation of land when greater land use raises current output but diminishes biodiversity.

Setup. We consider a simple two-period model that features both standard investment in physical capital and land use u. Equivalently, the share $1-u$ of land that is not used for production can be viewed as an investment in the conservation of natural capital. Given initial capital, K_0, a vector of the initial number of species per function $\boldsymbol{s}_0$, and a vector of the initial abundances in each function, $\bar{\boldsymbol{n}}_{\mathbf{0}}$, at time 0 the country's planner chooses 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.

Land Use and Ecosystem Services. Land use u increases present-day production, but at a cost to future ecosystem services E_1. This cost comes from two channels mirroring the findings from Liang, Rudik and Zou (2021), who document that "*shocks in economic production [...] led to a significant reduction in species abundance, diversity, and stability.*"

Channel (i): 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:

$$\bar{n}_{g,1}(u) = (1-u)\bar{n}_{g,0}. \tag{21}$$

Channel (ii): Second, land use negatively affects biodiversity in function g according to the following reduced-form specification (see, for example, Rosenzweig, 1995; IPBES, 2019; Johnson et al., 2021):

$$s_{g,1}(u) = s_{g,0} - \delta u. \tag{22}$$

Specifically. 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, consistent with the ecology finding 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).[24] In turn, as discussed in Section

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[24] 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

2, species loss affects ecosystem service production through three distinct forces that are all captured in equation (23). The parameter ϕ determines (i) the net abundance loss above and beyond the one captured by equation (21) that comes from a reduction in niche differentiation in resource absorption, and (ii) the reduction in function-level productivity that results from a decline niche differentiation in service performance. In addition, the parameter σ captures the third force, the additional output-effects from imbalances in biodiversity across the complementary ecosystem functions.

Combining with equations (7) and (8), future ecosystem services are as follows, where land use u appears twice in equation (23) to reflect the two channels through which it affects ecosystems:

$$E_1 = \left\{ \sum_g \left[\bar{E}_{g,0}(1-u) \left[s_{g,0} - \delta u \right]^{\phi_g} \right]^{\frac{\sigma-1}{\sigma}} \right\}^{\frac{\sigma}{\sigma-1}}. \tag{23}$$

Model Solution. We denote by $\eta_{X,t} = \frac{\partial \log Y_t}{\partial \log X_t}$ the elasticity of date-t output to any factor X_t (except in the Cobb-Douglas case, $\eta_{X,t}$ is endogenous and needs to be determined as part of the optimal solution). The optimal investment in physical capital can be expressed as an optimal savings rate:

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

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).

The most intuitive way to write the optimality condition with respect to land use is 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 between the two assets. At the optimum, equalizing the marginal returns on these two forms of capital implies that optimal conservation must satisfy

$$1 - u^* = \Lambda \frac{d \log E_1}{d \log(1-u)}, \tag{24}$$

where

$$\Lambda = \frac{\beta \eta_{E,1}}{\eta_{L,0} \left(1 + \beta \eta_{K,1}\right)} \tag{25}$$

is 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 level. Similarly, a higher elasticity of date-0 output to land use will lead to lower optimal land conservation. Of course, except in the Cobb-Douglas case ($\xi \to 1$), Λ itself is determined in equilibrium, and Appendix C.5 fully characterizes it. Besides Λ, the key object in the optimality condition in equation

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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.

(24) is the elasticity of ecosystem services to land conservation (which is also an equilibrium object that depends on u^*). Combining equations (23) and (24), we can express the optimal conservation $1-u^*$ as:

$$1 - u^* = \Lambda \times \Big\{ \underbrace{1}_{\text{Channel (i)}} + \underbrace{\delta(1-u^*)\mathcal{F}(\boldsymbol{s}_1)}_{\text{Channel (ii)}} \Big\}, \tag{26}$$

featuring the two channels by which land use affects ecosystem services. This gives the following result:

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

$$1 - u^* = \min\left\{1, \frac{\Lambda}{1 - \Lambda\delta\mathcal{F}(\boldsymbol{s}_1)}\right\}, \tag{27}$$

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 (27) 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 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 strength of the effect depends 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 (27) 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 comparative statics in Proposition 3.[25] As shown in Section 2.2, a lower substitutability σ between functions raises fragility and therefore optimal conservation. Optimal conservation decreases with initial biodiversity $\boldsymbol{s}_0$, as a more biodiverse economy has more room to deplete its natural capital before suffering harmful economic effects. Optimal conservation also increases with the importance of ecosystem services in production a_E and with patience β.

Finally, the parameter ξ, that determines the degree of complementarity between physical and natural capital (see section 3), has direct implications for how optimal policy varies with the stock of capital. For example, the case of "strong sustainability" ($\xi < 1$) implies that capital-rich countries, with a higher K_0, should invest more in biodiversity preservation. 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. That said, the general formulation of optimal land use of Proposition 3 is valid regardless of the specific value of ξ.

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[25] In Appendix C.6 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 ($s_{g,0} = s_0$ for all g).

Extension 1: Targeted Land Use. A key challenge specific to biodiversity relative to the extraction of other exhaustible resources is that the complexity of ecosystem systems makes it difficult to fine-tune land use to preserve the most critical ecosystem functions. In Appendix C.7, we contrast our baseline results with an idealized setting in which the social planner can target conservation activities to specific functional groups. Intuitively, the economic gains from corrective policies can then 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.

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 is valuable per se. We also do not consider how biodiversity loss might affect nature's provision of 'cultural ecosystem services' such as recreational opportunities, which can enter households' utility functions directly without affecting output. Our framework can easily be expanded to incorporate such additional considerations through non-pecuniary benefits from nature conservation. In Appendix C.8, 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.

Other potential extensions. The goal of this section is to provide a simple illustrative case of how our model can be integrated in an intertemporal framework to guide optimal policy. There are however many additional dimensions of the problem that have not been included in our analysis and would be natural extensions of the model. For example, this section only considers a single ecosystem; adding a geographic dimension to the model would enable the study of the implications for externalities across geographical boundaries, the role of institutions in managing those externalities, as well as the effect of trade across locations on the joint evolution of biodiversity and the economy. There is also an important role for intertemporal externalities (e.g., the divergence between the private and social discount factors), which would naturally lead to the study of optimal taxation of activities that deplete biodiversity.

5 Conclusion

This paper advances our understanding of the economic effects of biodiversity loss by developing a tractable framework, grounded in ecological research, that models how species interact within and across ecosystem functions to generate the ecosystem services that enter economic production functions. The model highlights the non-linear relationship between species loss and economic activity, and yields several important implications.

First, the framework shows that the absence of large economic losses from past biodiversity declines does not mean future losses will be limited. On the contrary, past extinctions have increased ecosystem fragility, making additional species losses increasingly costly for the economy. Consistent with this prediction, we find that components of a country's biodiversity risk exposure are already reflected in asset prices today. Policymakers should therefore weigh the intertemporal trade-offs of biodiversity loss, even when short-run 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. Our framework provides a way to quantify the marginal economic value of different species, which can help guide policy decisions around Pigouvian taxes, conservation efforts, the design of biodiversity offsets, and the design and valuation of financial contracts such as debt-for-nature swaps and blue bonds.

Our analysis represents only a first step in modeling and measuring aggregate biodiversity risk and its 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, which 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, as briefly mentioned in the last section, 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 Drupp and Hänsel, 2021; Giglio et al., 2025*b*, for first steps).

In addition to potential modeling enhancements, further progress on the measurement side is essential. The expanding availability of species-level biodiversity data holds great promise for estimating and calibrating models like the one we develop—an important step on the path to deriving concrete policy implications—though substantial empirical work is still needed to bring such models fully to the data.

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A Biodiversity Loss and Economic Activity - Case Studies

In this Appendix, we discuss several specific examples in which biodiversity loss has been shown to have large-scale economic and social costs. We first summarize well-identified evidence that shows that losses of individual keystone species can have meaningful negative effects across a range of metrics. We then explore several examples of local ecosystem collapse, and highlight the large negative effects of these events on the affected societies and economies.

Loss of Keystone Species. As discussed in Section 2.1, the concavity of ecosystem service production with respect to the number of species in a function gives rise to *keystone species*, the last remaining species performing a key ecosystem function. The loss of such species can result in significant social and economic costs. Beyond the loss of vultures in India discussed above, other examples further highlight the broad impacts of keystone species losses. For instance, Frank et al. (2024) examines the consequences of the large-scale eradication of sparrows during China's "Four Pests Campaign" (FPC) in 1958, which attempted to improve agricultural productivity by eliminating flies, mosquitoes, rats, and sparrows. Within two years, the FPC led to the local extinction of sparrows in China. However, sparrows served as a natural form of pest control, helping to regulate locust populations that threatened crops. In their absence, pest numbers soared, crippling crop yields. Frank et al. (2024) conclude that '*back of the envelope calculation suggests that sparrow killing can account for 19.6% of the national crop yield reduction during the Great Famine*," which, in turn, exacerbated mortality rates. Another example comes from the impact of white-nose syndrome on insect-eating bats in the United States. As documented in Frank (2024), the average mortality rate in bat colonies affected by this disease has exceeded 70% since its emergence in 2006. The rapid decline in bat populations weakened the ecosystem's natural pest control function, leading farmers in impacted areas to "*increase their insecticide use by 31.1%, on average*," causing a 7.9% increase in infant mortality rates. These cases illustrate how the loss of keystone species can have profound effects on both ecosystems and human populations.

Local Ecosystem Collapse. In extreme cases, local losses of key ecosystem functions can lead to the collapse of entire ecosystems. A prominent example of such an ecological collapse is the decline of the Aral Sea ecosystem. Once one of the world's largest inland bodies of water, the Aral Sea experienced a dramatic decline in water levels due to large-scale irrigation projects in the 1960s that diverted its primary water sources. This disruption led to the near-complete desiccation of the sea, as well as increased salinity in its remnants, creating "*an environment that is unsuited to native plant and animal species*". The local extinction of tigers and Bukhara deer, the imminent disappearance of ten bird types in the south part of the Aral region, and the vanishing of 12 out of 28 fish types are all linked to this initial shock (Janobiddinov, 2024). Micklin (2007) shows how this ecosystem collapse led to the destruction of the substantial Aral fishing industries and the unemployment of tens of thousands of people. He also highlights how "*strong winds blow sand, salt, and dust from the dried bottom of the Aral Sea*", so "*salts [...] settle on natural vegetation and crops*," such that "*plants are killed outright [or] more commonly, their growth (and for crops, yields) is substantially reduced*." Additionally, "*the population living in the so-called ecological disaster zone around the sea suffers acute health problems*," including "*respiratory and digestive afflictions and possibly cancer from inhalation and ingestion of blowing salt and dust*." Ultimately, the collapse of the Aral ecosystem resulted in a dramatic population declines in towns like Muynak, once the largest city on the Aral Sea with a population of close to 30,000, but now with only approximately 13,500 inhabitants (Hanks, 2021).

Another ecological disaster with large-scale economic consequences was the American Dust Bowl, which devastated vast areas of the Great Plains. The region's ecological resilience was initially weakened by the widespread extermination of the plains bison, which had played a vital role in maintaining prairie ecosystems, in particular by helping native grasses develop deep root systems that stabilized the soil and retained moisture (Ratajczak et al., 2022). Without these grazers, the ecosystem became less resilient, and combined with decades of unsustainable farming practices such as deep plowing and monoculture cultivation, the region's native grasses were lost, leaving the soil exposed and vulnerable to erosion. When a severe drought struck in the 1930s, strong winds swept up the dry, bare soil, forming massive dust storms that occurred throughout the decade. According to Hornbeck (2012), "*farmland was left severely eroded*," and "*more-eroded counties experienced large and permanent relative declines in agricultural land values: the per acre value of farmland declined by 30 percent in high-erosion counties [. . .] relative to changes in low-erosion counties*." This led to a "Dust Bowl exodus", where in the 1930s, "*total population declined between 3% and 8% in the five central Plains states*," with high-erosion counties experiencing a 12% decline in population relative to low-erosion counties. Noghanibehambari and Fletcher (2024) additionally find that the effects of the Dust Bowl extended into long-term health and economic outcomes, where "*individuals born in high-erosion counties after the 1930s lived 0.85 fewer months*," and "*experienced large and significant reductions in adulthood income*."

Moreover, the ongoing Chinese Dust Bowl serves as a stark reminder that such ecological disasters are not confined to the past. The root causes of the Chinese Dust Bowl echo those of the American Dust Bowl, with "*cultivation, grazing, destruction or harvesting of herbaceous vegetation and logging forests to produce firewood and rural construction materials*" being the dominant cause of widespread desertification (Feng et al., 2015). By 2010, over 57% of the land in Ningxia Hui Autonomous Region, covering 2.97 million hectares, had been degraded. This left dunes exposed and prone to shifting, resulting in over 3 million people suffering from frequent sandstorms and hazardous dust pollution (World Bank, 2021). The economic effects of such desertification in China are profound, with Lu and Wang (2003) estimating direct economic losses of 7.7 billion USD annually. As Rechtschaffen (2017) documents, China "*lost 6.2% of its farmland between 1997 and 2008*, exacerbating the country's food security crisis. Furthermore, "*as towns get swallowed by deserts, so do their economies*," with desertification forcing the large-scale resettlement of populations. Between 2003 and 2008, "*650,000 people living in China's Inner Mongolia province were forcibly resettled*," with immediate and large-scale costs to local economic activity.

All three case studies—the Aral ecosystem collapse, and the Dust Bowls in the United States and China—highlight how ecosystem collapse, often facilitated by the degradation of biodiversity due to human interventions, can cause large social and economic costs.

B Empirical Analysis - Further Details

In this Appendix, we provide further details on the data source and data construction steps behind the results presented in Section 3.3 of the main paper. We also present additional results that highlight the robustness of our baseline findings to variations in the empirical specification.

B.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-country-year levels from 2001 to 2021. Here, area scores are defined as the product of habitat suitability scores (ranging continuously from 0 to 1) and habitat size scores. 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, and a species' connectivity score in a given country-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. To assess the extent to which habitat scores capture similar variation as area scores, we report the correlation between across-suborder dispersion in 2012 for the two measures in Table A.10. The correlation is 26%, suggesting that habitat scores capture distinct information relative to area scores.

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 their 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—for some species in the Map of Life data that are not in the TetrapodTraits data, we are able to infer their taxonomic classification by matching the genus (the first word of its scientific name) with the genera present in the TetrapodTraits data, thereby obtaining the order, suborder and family information. From there, we can 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 2012. In Table A.3, we report summary statistics by country. For example, for Argentina we have data on 1,119 unique species belonging to 132 families, 48 suborders, and 40 orders. Across these species, the 2012 area scores have a standard deviation of 4.58; the within-suborder average area scores have a standard deviation of 1.47 across suborders. In Figures B.2 and B.4, we map the across-suborder and across-family means and standard deviations of area scores in 2012 for countries in our regression sample. In Table A.4, we report the count, across-group mean, and across-group standard deviation of area scores in 2012 for countries outside our sample.

Our baseline measure for the across-function dispersion of biodiversity losses is the across-suborder standard deviation of the area score in 2012, as it aligns with roughly the midpoint of our CDS data. We also compute analogous dispersion measures for 2021, which we use in robustness checks and in the construction of current $BiodiversityRiskExposure$. Table A.5 presents 2021 summary statistics by country, and Figures B.3 and B.5 show the maps of across-suborder and across-family means and standard deviations. Summary statistics in 2021 for countries outside the sample are shown in Table A.6. To assess the robustness to different choices, we calculate the correlation and Spearman rank correlations with 12 combinations of the following specifications: three score types (SD, p10, and min area), two taxonomic levels (suborder and suborder), and two time points (2012 and 2021). These correlations presented in Tables A.7 and A.8 reveal large 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 3.3, 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".[26] 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. The "Ecosystem Services" category encompasses 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: the "Fish Stock Status" measures *"the percentage of a country's total*

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[26] 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.

catch that comes from overexploited or collapsed fish stocks".; the "Marine Trophic Index" (MTI) captures the *"ecological pressures on fish stocks"* by analyzing which trophic level or food web levels a country's fishing industry is targeting; and the "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. The rank of each country within our sample is shown in parentheses, with better ranks corresponding to lower biodiversity destruction scores. The indicators comprising the EPI are available as of 2022, but there are also versions 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 analysis we use this value as of 2012, which roughly aligns with the midpoint of our CDS data series. Table A.9 shows that the EPI-based measure of biodiversity obtained at the baseline is very similar to the measure based on 2022 data. Table A.10 further shows that the baseline measure is correlated at 71% with its 2022 value, and at 91% with the average of the 2012 and 2022 values. Our robustness check in Table A.11 also shows that our results are similar when using the 2022 value, and using the average of the baseline and 2022 values.

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.

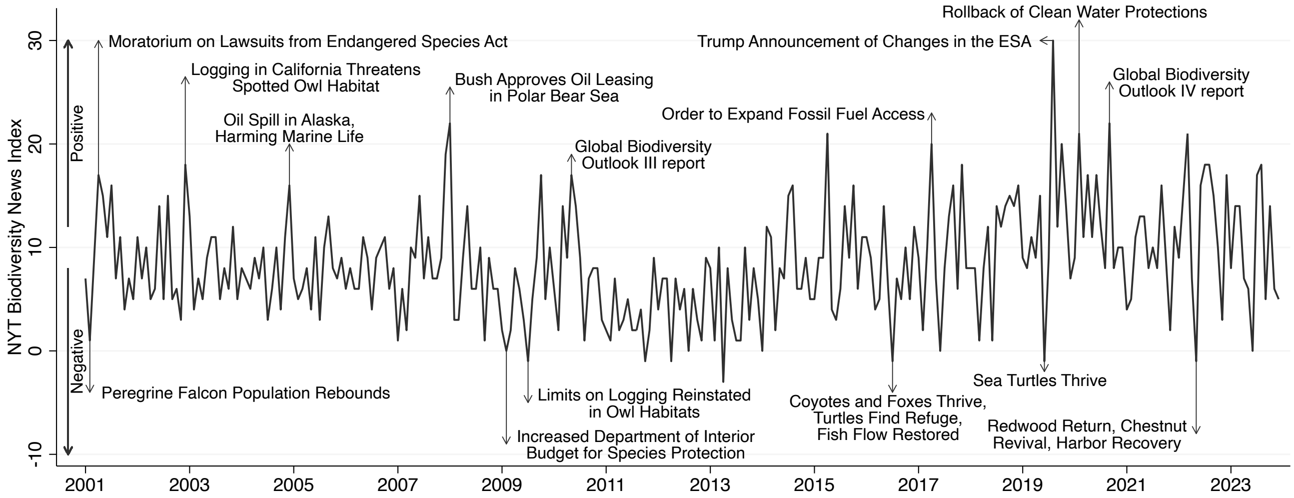
Correlation Across Measures. Table A.10 shows the correlation between our different country level measures. Our main measure of average biodiversity loss, *Biodiversity Destruction Score-2012*, is essentially uncorrelated with the *Across-Suborder Dispersion of Area Scores in 2012*. This suggests that our 2 measures capture completely different concepts. Our EPI-based measure captures how much biodiversity has degraded in a given country relative to its original state, while our Map of Life-based measure captures the dispersion of this biodiversity degradation in a given country relative to its original state.

Table A.10 also shows the correlation between alternative measures for a country's state of biodiversity. The *Biodiversity Destruction Score-2022* measure uses information from 2022 only, and has a 71% correlation with 2012 values, while *Biodiversity Destruction Score–Avg*, which averages the 2012 and 2022 values, has a 91% correlation with 2012 and a 94% correlation with 2022. Using only the EPI indicators from the Biodiversity & Habitat category (excluding those from the ecosystem category) yields a correlation of 43%, suggesting that ecosystem services and fisheries capture different aspects of a country's natural resources. The *Environmental Vulnerability Index* is barely correlated with our baseline measure.

The correlation is higher at 46% when only biodiversity indicators of the EPI are included. The *Across-Suborder Dispersion of Area Scores* has an 91% correlation with the *Across-Family Dispersion of Area Scores*, suggesting that dispersion patterns remain consistent over different taxonomic levels. However, the *Across-Suborder Dispersion of Habitat Scores* only show a 26% correlation with the previous two measures, indicating that habitat connectivity does not fully align with habitat size. These measures of dispersion remain mostly uncorrelated with the *Biodiversity Destruction Score* 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 measure news coverage of biodiversity losses, we use the NYT Biodiversity News Series produced by Giglio et al. (2023), which is from 2000 to 2023. 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 show the news index aggregated to the monthly level in Figure B.1, with important events labelled. In our empirical specification, we use the news series aggregated to the weekly level using Friday observations, to align the timing of news measurement with the beginning of the trading week. We then follow Giglio et al. (2023), as well as prior work by Engle et al. (2020) and Alekseev et al. (2025), and use residuals from an AR(1) process fitted to the news series as our measure of the unanticipated component of news.

Figure B.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.

CDS Data. We obtain sovereign CDS data from Markit and include all CDS on sovereign debt contained in the database, identified by matching CDS tickers to countries. 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, but otherwise use 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 USD and EUR, 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, allowing us to use the par spread for the entire sample period. Similarly to the news index, we aggregate CDS data at a weekly frequency using Friday observations.

B.2 Robustness Tests

Table A.11 explores the robustness of our results to adjustments in data construction choices. The first column modifies the specification in column 2 of Table 1 by using the *Biodiversity News* index directly, rather than its AR(1) innovations. Column 2 adjusts the winsorization threshold for percent changes in CDS spreads to the 2nd and 98th percentiles. Column 3 restricts the sample to USD-denominated CDS contracts. In column 4, the dispersion measure is updated to reflect 2021 values rather than 2012. Columns 5 and 6 replace the standard deviation of area scores across suborders with alternative statistics: the 10th percentile and minimum value of area scores across suborders, respectively. These measures are recoded so that lower scores, which indicate worse outcomes, correspond to higher values in the regression. Column 7 updates the *Biodiversity Destruction Score* to use 2022 data, while column 8 uses the average of the 2012 and 2022 values. The results are broadly consistent across specifications.

Table A.1: Biodiversity Destruction Score By Country in 2012

	Biodiversity Destruction Score	
	Score	**Global Rank**
Africa	**67.08**	
Ghana	77.39	(10)
Kenya	74.51	(20)
South Africa	74.12	(24)
Nigeria	73.21	(28)
Rwanda	69.14	(49)
Cameroon	68.13	(54)
Tunisia	67.54	(60)
Zambia	65.29	(68)
Angola	64.09	(70)
Morocco	63.02	(73)
Algeria	62.82	(74)
Egypt	57.65	(85)
Côte d'Ivoire	55.06	(88)
Asia	**58.67**	
Indonesia	80.29	(5)
Malaysia	77.52	(9)
Thailand	74.64	(19)
Turkey	73.01	(30)
Lebanon	72.55	(32)
Korea	70.35	(46)
Vietnam	69.20	(48)
Cyprus	68.70	(52)
China	67.82	(56)
Japan	67.70	(58)
Taiwan	67.65	(59)
Philippines	65.69	(67)
Mongolia	62.40	(77)
Israel	61.80	(78)
Sri Lanka	61.70	(79)
India	61.09	(81)
Pakistan	59.75	(84)
Oman	56.62	(86)
Kazakhstan	54.83	(89)
Iraq	51.42	(91)
Azerbaijan	49.29	(92)
Singapore	48.39	(93)
Qatar	35.34	(94)
Bahrain	33.17	(95)
Jordan	32.18	(96)
Saudi Arabia	30.95	(98)
United Arab Emirates	30.16	(99)
Europe	**68.18**	
Portugal	82.85	(2)
Spain	77.53	(8)
Belgium	75.66	(13)
Malta	75.60	(15)
United Kingdom	75.07	(16)
Netherlands	74.81	(18)
Ireland	74.33	(23)
Denmark	73.84	(25)
France	73.50	(26)
Ukraine	73.15	(29)
Poland	72.86	(31)
Hungary	72.30	(34)
North Macedonia	71.83	(36)
Belarus	71.75	(37)
Greece	71.31	(39)
Sweden	71.28	(40)
Russia	71.26	(41)
Italy	71.21	(42)
Lithuania	70.63	(45)
Austria	69.47	(47)
Croatia	69.08	(50)
Czechia	68.43	(53)
Germany	68.05	(55)
Montenegro	67.15	(62)
Bulgaria	66.51	(64)
Slovakia	65.71	(66)
Finland	63.79	(71)
Serbia	62.78	(75)
Latvia	62.73	(76)
Slovenia	61.44	(80)
Estonia	60.34	(82)
Norway	60.18	(83)
Switzerland	56.12	(87)
Romania	52.05	(90)
Iceland	31.77	(97)
North America	**74.81**	
Panama	80.76	(3)
Trinidad and Tobago	80.30	(4)
El Salvador	79.62	(6)
U.S.A.	78.19	(7)
Guatemala	76.98	(11)
Costa Rica	75.61	(14)
Canada	74.41	(22)
Barbados	73.45	(27)
Jamaica	72.20	(35)
Mexico	71.17	(43)
Belize	67.76	(57)
Dominican Republic	67.31	(61)
Oceania	**71.33**	
New Zealand	74.95	(17)
Australia	72.51	(33)
Fiji	66.54	(63)
South America	**71.09**	
Uruguay	82.86	(1)
Argentina	76.18	(12)
Chile	74.42	(21)
Colombia	71.51	(38)
Ecuador	71.03	(44)
Brazil	68.96	(51)
Venezuela	66.39	(65)
Bolivia	64.91	(69)
Peru	63.56	(72)

Note: The table shows the "Biodiversity Destruction Score" by country in 2012. 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: Biodiversity Destruction Score By Country in 2022

	Biodiversity Destruction Score				
	Score	**Global Rank**		**Score**	**Global Rank**
Africa	**72.14**		France	75.42	(32)
Ghana	83.61	(5)	United Kingdom	75.00	(35)
Nigeria	79.63	(14)	Germany	74.99	(36)
Kenya	78.53	(17)	Belarus	74.97	(37)
Cameroon	77.84	(19)	Czechia	74.57	(40)
Rwanda	75.94	(28)	Slovakia	74.42	(41)
South Africa	75.06	(34)	Italy	74.41	(42)
Morocco	74.87	(38)	Ukraine	73.86	(43)
Algeria	72.53	(49)	Greece	73.47	(46)
Zambia	70.26	(57)	Latvia	71.52	(51)
Tunisia	69.52	(60)	North Macedonia	71.23	(52)
Angola	67.12	(71)	Sweden	70.88	(54)
Egypt	57.50	(85)	Estonia	70.78	(55)
Côte d’Ivoire	55.45	(87)	Hungary	69.39	(61)
Asia	**63.28**		Montenegro	68.89	(66)
Qatar	89.43	(1)	Finland	67.01	(72)
Malaysia	88.86	(2)	Austria	66.76	(74)
Vietnam	82.35	(6)	Croatia	66.67	(75)
Thailand	82.02	(7)	Bulgaria	65.88	(76)
Indonesia	80.59	(11)	Switzerland	64.50	(77)
Korea	79.51	(15)	Slovenia	62.29	(80)
Turkey	78.47	(18)	Norway	60.21	(83)
Cyprus	77.05	(22)	Serbia	59.29	(84)
China	75.80	(30)	Romania	53.21	(90)
Lebanon	74.71	(39)	Iceland	41.59	(93)
Japan	73.79	(44)	Malta	23.10	(99)
India	72.58	(48)	**North America**	**71.56**	
Taiwan	70.37	(56)	Guatemala	80.72	(10)
Philippines	69.15	(64)	U.S.A.	76.12	(27)
Sri Lanka	67.14	(70)	Costa Rica	75.39	(33)
Mongolia	62.47	(79)	Jamaica	72.62	(47)
Israel	61.79	(81)	Belize	71.01	(53)
Kazakhstan	55.72	(86)	Trinidad and Tobago	70.16	(58)
Singapore	54.68	(88)	Panama	69.76	(59)
Oman	53.54	(89)	Mexico	69.28	(62)
Pakistan	52.61	(91)	Canada	69.27	(63)
Azerbaijan	44.34	(92)	El Salvador	69.09	(65)
Jordan	36.69	(94)	Dominican Republic	67.84	(67)
Bahrain	33.17	(95)	Barbados	67.46	(69)
Iraq	31.35	(96)	**Oceania**	**73.17**	
Saudi Arabia	31.12	(97)	New Zealand	76.72	(24)
United Arab Emirates	29.15	(98)	Australia	75.86	(29)
Europe	**69.65**		Fiji	66.94	(73)
Portugal	84.58	(3)	**South America**	**72.99**	
Spain	81.10	(8)	Uruguay	84.41	(4)
Denmark	81.06	(9)	Argentina	79.16	(16)
Poland	80.11	(12)	Bolivia	77.20	(21)
Belgium	79.94	(13)	Brazil	76.50	(26)
Ireland	77.40	(20)	Colombia	73.60	(45)
Netherlands	77.03	(23)	Ecuador	72.40	(50)
Lithuania	76.71	(25)	Chile	67.69	(68)
Russia	75.51	(31)	Venezuela	64.19	(78)
			Peru	61.73	(82)

Note: The table shows the “Biodiversity Destruction Score” by country in 2022. 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.3: 2012 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	102.51	4.29	83	102.50	3.50	37	102.89	3.13	31	103.21	3.14
Angola	1079	99.88	2.03	145	99.83	0.89	53	99.90	0.61	44	99.81	0.57
Argentina	1119	98.29	4.58	132	98.14	3.17	48	98.66	1.47	40	98.66	1.51
Australia	1080	99.58	1.55	120	99.66	0.84	42	99.70	0.56	35	99.78	0.51
Austria	250	99.50	1.86	70	99.59	1.01	32	99.57	0.82	28	99.61	0.85
Azerbaijan	313	99.96	0.94	80	99.91	0.50	36	99.91	0.42	29	99.96	0.39
Bahrain	29	96.81	7.44	20	97.20	7.27	12	96.29	5.15	10	96.78	5.49
Barbados	32	99.28	4.34	23	99.11	4.19	15	99.34	5.00	10	99.77	3.67
Belarus	218	99.60	0.87	67	99.62	0.53	30	99.65	0.48	26	99.63	0.43
Belgium	196	98.27	2.45	64	98.33	1.84	30	98.17	1.95	26	98.21	2.01
Belize	556	98.60	3.70	107	98.59	2.44	42	98.58	2.20	34	98.70	2.05
Bolivia	1690	99.18	2.71	143	99.24	1.95	47	99.54	1.88	38	99.70	2.01
Brazil	2463	98.19	3.54	155	98.35	1.62	47	98.66	1.19	38	98.66	1.24
Bulgaria	296	99.73	1.24	78	99.72	0.87	35	99.72	0.77	29	99.74	0.76
Cameroon	1038	99.56	2.79	144	99.12	5.34	50	99.35	2.03	41	99.60	1.08
Canada	409	99.53	2.08	86	99.57	1.17	33	99.46	0.99	28	99.55	0.95
Chile	306	99.59	2.31	75	99.49	1.75	33	99.31	2.35	28	99.69	0.81
China	1756	98.90	4.13	156	98.81	3.95	48	98.09	5.33	39	99.07	1.62
Colombia	2462	98.83	2.45	159	98.96	1.53	50	99.17	1.34	41	99.22	1.33
Costa Rica	1061	99.15	2.72	127	99.54	1.72	44	99.59	1.40	36	99.79	1.39
Croatia	292	99.59	0.86	82	99.63	0.53	36	99.63	0.41	30	99.67	0.40
Cyprus	112	99.34	1.91	50	99.09	1.70	28	98.98	1.77	22	99.25	1.54
Czech Republic	219	99.24	1.08	68	99.24	0.70	31	99.11	0.60	27	99.09	0.60
Côte d'Ivoire	717	98.00	7.05	131	98.13	3.56	48	98.41	2.82	40	98.33	2.94
Denmark	175	99.64	0.79	64	99.64	0.45	29	99.59	0.40	25	99.62	0.39
Dominican Republic	208	100.14	2.21	66	99.99	1.68	31	100.09	1.37	26	100.09	1.45
Ecuador	1929	98.89	2.59	149	98.69	2.22	50	98.61	2.27	41	98.72	2.25
Egypt	241	100.51	2.68	81	100.64	2.50	36	100.94	3.04	30	101.12	3.28
El Salvador	521	99.48	1.83	104	99.49	1.17	42	99.50	0.95	34	99.43	0.99
Estonia	191	100.13	3.12	64	100.30	2.47	30	100.36	2.44	26	100.53	2.57
Fiji	34	100.01	0.77	19	100.16	0.86	11	100.34	1.10	9	100.42	1.21
Finland	179	100.51	3.81	61	100.66	1.94	28	100.43	2.01	25	100.50	2.12
France	336	99.52	1.11	93	99.62	0.81	38	99.60	0.62	32	99.53	0.51
Germany	264	99.17	1.19	76	99.20	0.80	33	99.11	0.80	29	99.12	0.80
Ghana	704	100.46	2.84	134	100.53	1.64	47	100.68	1.24	39	100.64	1.18
Greece	326	99.82	0.69	84	99.88	0.49	37	99.87	0.38	30	99.84	0.40
Guatemala	878	96.62	6.62	118	97.02	3.93	43	97.16	3.18	35	96.97	3.36
Hungary	242	99.53	1.70	69	99.48	1.13	33	99.47	1.38	28	99.50	1.46
Iceland	29	100.00	0.00	15	100.00	0.00	8	100.00	0.00	8	100.00	0.00
India	1455	99.67	2.47	151	99.68	1.01	48	99.52	1.06	40	99.62	0.79
Indonesia	2216	98.14	6.64	171	99.05	6.12	56	98.45	2.96	45	98.52	3.21
Iraq	301	100.23	1.23	82	100.27	0.85	34	100.12	0.63	28	100.19	0.66
Ireland	94	100.53	1.25	44	100.35	0.93	22	100.18	0.81	22	100.18	0.81
Israel	258	99.66	1.66	82	99.56	1.27	33	99.62	1.30	27	99.72	1.41
Italy	331	99.57	1.34	89	99.62	0.90	37	99.57	0.65	31	99.60	0.63
Jamaica	143	98.99	1.92	54	99.23	1.74	25	99.07	0.61	22	99.10	0.60
Japan	325	99.12	1.60	93	99.20	1.27	36	99.12	1.04	30	99.13	0.99
Jordan	241	99.51	1.42	76	99.43	1.15	30	99.33	1.02	24	99.47	0.92
Kazakhstan	397	100.92	1.80	91	100.84	1.50	36	100.95	1.03	29	101.15	0.80
Kenya	1182	100.02	1.31	154	100.07	0.56	53	100.07	0.44	44	100.05	0.43
Latvia	197	99.76	3.19	65	100.11	2.32	30	100.14	2.40	26	100.24	2.57
Lebanon	212	99.89	1.13	78	99.78	0.97	32	99.75	1.13	26	99.76	1.24

Table A.3: 2012 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
Lithuania	194	99.72	1.10	65	99.80	0.53	30	99.78	0.59	26	99.77	0.63
Macedonia	260	99.48	1.69	75	99.55	1.13	35	99.56	0.93	29	99.58	0.95
Malaysia	1075	96.94	7.64	132	98.61	6.41	46	98.05	4.07	37	98.47	4.31
Malta	23	99.12	2.50	17	99.19	2.17	13	99.43	1.95	10	99.62	1.60
Mexico	1593	98.70	3.09	145	98.94	1.52	50	98.94	1.26	41	98.89	1.33
Mongolia	289	100.68	2.85	68	100.49	1.97	30	100.78	1.20	27	100.85	1.24
Montenegro	251	98.83	1.97	74	99.01	1.26	35	98.98	1.26	29	99.09	1.07
Morocco	294	100.48	2.57	94	100.55	1.62	39	100.91	1.84	33	101.02	1.84
Netherlands	195	98.72	2.10	66	98.68	1.46	30	98.49	1.39	26	98.47	1.41
New Zealand	105	99.49	2.28	40	99.46	1.46	24	99.56	1.19	22	99.54	1.22
Nigeria	933	99.70	2.77	145	99.50	2.25	53	99.52	1.94	44	99.49	1.96
Norway	177	100.64	2.26	62	100.64	1.92	29	100.47	2.22	26	100.57	2.31
Oman	146	100.10	0.62	60	100.14	0.50	26	100.11	0.28	22	100.15	0.27
Pakistan	576	99.97	3.32	115	100.15	1.69	39	99.90	1.60	32	100.08	1.47
Panama	1155	98.88	2.68	134	99.12	1.48	43	99.05	1.18	36	99.14	1.20
Peru	2048	99.12	2.56	155	99.37	1.04	50	99.58	0.60	41	99.59	0.64
Philippines	803	98.98	3.13	113	99.25	1.45	40	99.29	0.90	32	99.35	0.84
Poland	240	99.58	0.80	69	99.58	0.48	30	99.53	0.44	26	99.50	0.44
Portugal	264	99.32	1.62	86	99.47	1.54	38	99.36	1.56	31	99.55	1.60
Qatar	46	100.35	2.33	28	100.65	2.71	17	101.18	3.33	13	101.60	3.73
Romania	288	99.46	1.24	79	99.41	0.99	35	99.44	0.92	30	99.37	0.94
Russia	644	99.96	2.34	110	99.92	1.18	39	100.11	1.35	32	99.91	0.61
Rwanda	764	99.96	0.86	124	100.02	0.60	46	99.95	0.21	38	99.96	0.21
Saudi Arabia	239	100.46	2.79	80	100.16	1.26	32	100.38	1.26	26	100.49	1.38
Serbia	272	99.68	1.46	74	99.69	0.93	33	99.71	0.79	28	99.69	0.81
Singapore	393	88.95	13.23	98	88.79	10.30	38	88.70	8.84	31	87.67	8.83
Slovakia	230	99.43	1.41	69	99.39	0.71	31	99.27	0.69	26	99.23	0.72
Slovenia	260	99.56	1.12	74	99.61	0.90	34	99.54	0.85	29	99.43	0.60
South Africa	952	99.64	1.65	145	99.66	1.03	53	99.82	1.13	43	99.69	0.40
South Korea	189	99.29	2.80	74	99.39	2.54	31	99.40	2.32	26	99.21	2.35
Spain	353	99.60	1.19	97	99.59	0.89	42	99.52	0.89	35	99.66	0.76
Sri Lanka	399	99.82	1.56	104	99.95	0.89	42	99.81	0.75	35	99.92	0.70
Sweden	193	100.41	3.85	65	100.65	2.24	29	100.58	2.46	25	100.73	2.62
Switzerland	230	98.91	1.45	64	99.03	1.05	30	98.90	0.83	26	98.92	0.83
Taiwan	373	98.88	1.45	97	98.85	1.21	34	98.73	0.90	28	98.72	0.91
Thailand	1254	98.16	5.02	140	98.66	2.49	47	98.40	1.91	39	98.67	1.82
Trinidad and Tobago	432	98.70	1.74	103	98.68	1.26	41	98.80	0.73	33	98.78	0.70
Tunisia	230	102.44	5.01	80	102.32	3.69	35	102.25	3.17	29	102.29	3.25
Turkey	453	99.48	2.75	97	99.55	0.75	39	99.52	0.67	32	99.50	0.71
Ukraine	299	99.41	1.60	79	99.38	1.15	36	99.36	1.04	30	99.30	1.11
United Arab Emirates	104	99.99	0.28	52	99.99	0.19	22	100.01	0.14	18	100.02	0.15
United Kingdom	170	99.42	1.11	59	99.46	0.68	29	99.40	0.53	26	99.42	0.53
United States	1037	99.14	4.19	131	99.31	2.47	45	99.57	1.34	37	99.61	1.45
Uruguay	370	99.63	2.92	90	99.85	1.92	39	99.87	1.23	32	99.82	1.15
Venezuela	1677	99.51	1.41	143	99.59	0.96	45	99.76	0.62	37	99.77	0.60
Vietnam	1137	98.39	3.54	137	98.82	2.26	47	97.82	2.39	38	98.15	2.33
Zambia	829	99.98	1.12	139	99.93	0.70	50	100.06	0.54	41	100.14	0.45

Note: The table shows the count, as well as the mean and standard deviation of area scores across species, families, suborders and orders in 2012 for each country in our final regression sample.

Table A.4: 2012 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	100.22	3.06	91	100.25	1.04	32	100.34	1.09	26	100.42	0.92
Akrotiri and Dhekelia	48	99.00	2.21	30	98.76	1.91	18	98.62	1.64	13	98.74	1.86
Albania	265	99.42	1.05	78	99.50	0.67	35	99.47	0.71	29	99.49	0.75
Andorra	99	99.84	0.38	44	99.82	0.32	20	99.78	0.40	16	99.76	0.44
Anguilla	21	100.75	1.02	15	100.88	1.09	10	101.04	1.00	7	100.90	0.95
Antigua and Barbuda	36	101.90	2.45	23	101.68	2.38	14	101.54	2.28	13	101.43	2.33
Armenia	277	99.71	0.49	77	99.70	0.38	35	99.67	0.38	29	99.70	0.29
Aruba	28	99.63	1.39	21	99.47	1.48	14	99.56	1.67	12	99.56	1.79
Bahamas	114	101.48	1.73	47	101.39	1.49	26	101.37	1.65	23	101.22	1.65
Bangladesh	588	99.62	1.57	116	99.62	0.99	40	99.41	1.16	33	99.38	1.22
Benin	587	99.98	2.76	121	99.95	3.37	47	100.16	1.54	39	100.18	1.56
Bhutan	612	100.12	1.45	116	100.22	0.84	39	100.11	0.74	31	100.03	0.71
Bonaire, Sint Eustatius & Saba	51	100.37	2.17	33	100.42	2.06	17	100.36	1.09	13	100.32	1.01
Bosnia and Herzegovina	274	99.26	2.07	79	99.13	3.03	35	99.14	2.99	29	99.64	0.64
Botswana	643	100.32	1.44	131	100.22	0.93	49	100.36	0.65	40	100.40	0.61
British Virgin Islands	40	97.94	3.97	26	98.27	3.38	14	98.06	2.66	12	98.42	2.03
Brunei	616	99.22	1.83	108	99.38	0.78	40	99.11	0.71	32	99.04	0.75
Burkina Faso	472	100.01	3.02	117	100.13	2.16	44	99.96	2.03	37	99.71	1.81
Burundi	713	99.72	1.36	127	99.71	0.92	47	99.72	0.74	39	99.75	0.77
Cambodia	713	97.68	6.61	122	98.57	4.45	44	97.70	3.79	36	97.89	4.09
Cape Verde	15	100.04	0.89	10	100.04	0.67	7	100.04	0.75	7	100.04	0.75
Cayman Islands	48	99.79	2.90	24	99.79	2.08	14	100.16	2.66	11	99.75	1.88
Central African Republic	814	99.89	1.58	135	99.94	0.71	50	99.95	0.55	41	99.99	0.55
Chad	540	100.08	1.58	119	100.16	1.21	45	100.18	0.98	39	100.19	1.03
Comoros	56	99.99	1.16	28	99.99	1.01	13	100.09	0.71	10	99.94	0.50
Cuba	215	99.63	2.24	62	99.92	1.25	31	99.76	0.49	25	99.77	0.48
Curaçao	41	98.92	5.73	29	98.69	6.04	16	99.18	5.07	13	99.10	5.57
Dem. Rep. of the Congo	1376	99.78	2.92	148	100.01	1.39	55	99.97	1.20	46	100.09	1.25
Djibouti	226	98.66	2.37	90	98.63	2.01	37	98.75	1.46	32	98.72	1.56
Dominica	61	99.90	0.30	35	99.91	0.24	16	99.92	0.12	12	99.91	0.14
Equatorial Guinea	531	100.68	8.68	119	101.39	9.98	46	101.73	6.58	37	102.08	7.22
Eritrea	452	100.26	0.86	118	100.23	0.74	46	100.27	0.59	40	100.33	0.60
Ethiopia	872	100.18	0.96	137	100.17	0.58	47	100.21	0.40	39	100.21	0.36
Falkland Islands	32	99.53	0.43	24	99.61	0.43	13	99.62	0.42	12	99.59	0.42
French Guiana	829	100.05	3.29	120	100.06	1.88	43	100.12	1.10	35	100.05	0.83
French Polynesia	22	100.00	0.00	10	100.00	0.00	7	100.00	0.00	7	100.00	0.00
Gabon	630	100.10	1.39	128	100.06	0.70	47	100.08	0.64	38	100.11	0.69
Gambia	424	100.22	1.63	113	100.31	1.19	43	100.52	1.05	36	100.54	1.06
Georgia	297	99.75	0.43	80	99.71	0.35	38	99.66	0.42	31	99.70	0.34
Greenland	28	100.00	0.00	15	100.00	0.00	7	100.00	0.00	7	100.00	0.00
Grenada	56	99.28	2.85	32	99.07	3.21	16	99.67	1.18	13	99.60	1.30
Guadeloupe	66	99.42	2.01	38	99.33	1.92	18	99.34	1.15	14	99.51	0.79
Guernsey	20	97.50	3.78	17	97.39	3.59	12	97.17	3.98	12	97.17	3.98
Guinea	724	99.57	2.63	134	99.42	2.81	48	99.67	0.85	40	99.65	0.89
Guinea-Bissau	442	100.20	2.52	112	100.12	1.80	44	99.94	1.56	37	100.01	1.61
Guyana	1019	99.94	1.38	127	100.02	0.85	44	100.09	0.74	36	100.13	0.80
Haiti	204	98.80	1.86	65	98.89	1.24	31	98.82	0.94	26	98.92	0.96
Honduras	920	97.56	5.02	123	97.78	3.23	44	98.12	1.96	36	98.05	1.99
Hong Kong	276	98.80	3.67	86	98.48	3.11	36	98.98	3.12	28	98.60	2.85
Iran	506	100.73	2.16	100	100.84	1.53	37	100.98	1.49	31	101.18	1.51
Isle of Man	27	99.71	1.07	23	99.74	1.12	13	99.89	1.35	13	99.89	1.35
Jersey	36	99.04	2.90	23	98.62	2.01	14	98.54	1.95	14	98.54	1.95

Table A.4: 2012 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
Kosovo	244	99.62	0.81	72	99.63	0.57	34	99.59	0.63	28	99.62	0.52
Kuwait	71	100.37	3.13	37	100.45	3.53	19	100.91	4.61	14	101.37	5.34
Kyrgyzstan	237	100.13	1.05	74	100.08	0.76	34	99.99	0.64	29	100.01	0.69
Laos	970	98.34	4.73	126	99.13	3.25	44	98.17	3.02	35	98.79	2.51
Lesotho	370	99.75	1.05	109	99.76	0.73	44	99.72	0.63	35	99.85	0.41
Liberia	544	99.28	3.85	121	99.65	5.73	45	99.30	1.94	37	99.32	2.02
Libya	157	99.87	0.64	63	99.88	0.32	29	99.90	0.25	24	99.93	0.22
Liechtenstein	74	97.73	4.21	36	97.05	3.58	19	97.50	2.90	16	97.71	2.88
Luxembourg	157	98.67	1.45	57	98.66	1.10	29	98.70	0.98	25	98.73	1.01
Madagascar	464	96.73	6.62	78	98.62	3.47	35	97.80	3.18	30	97.80	3.38
Malawi	718	100.00	1.44	133	99.97	0.63	48	100.07	0.49	39	100.12	0.47
Mali	537	100.40	1.56	120	100.47	1.16	46	100.57	0.92	39	100.61	0.91
Martinique	75	99.35	1.14	43	99.32	1.29	22	99.17	1.59	17	99.11	1.81
Mauritania	374	100.38	1.94	110	100.52	1.62	45	100.42	1.74	39	100.55	1.80
Mauritius	17	99.02	1.85	14	98.98	1.67	8	99.11	1.78	7	99.31	1.25
Mayotte	31	100.36	1.00	20	100.33	0.97	12	100.13	0.93	9	100.07	0.99
Micronesia	26	99.98	0.05	14	99.97	0.06	9	99.97	0.07	8	99.96	0.07
Moldova	226	99.24	2.74	67	99.25	2.42	31	99.00	1.25	27	98.90	1.25
Montserrat	25	99.24	1.88	17	99.12	2.04	10	99.74	0.58	7	99.66	0.58
Mozambique	831	99.84	2.06	143	99.84	1.06	51	99.87	1.18	42	99.92	1.27
Myanmar	1294	98.61	5.09	143	98.79	3.20	48	98.59	2.63	40	98.77	2.73
Namibia	716	101.16	3.11	135	101.15	1.50	51	101.15	1.22	42	101.11	1.20
Nepal	713	99.94	0.41	119	99.95	0.30	41	99.95	0.37	33	99.89	0.16
New Caledonia	83	100.59	2.40	28	99.86	2.69	15	99.30	3.35	14	99.18	3.44
Nicaragua	848	96.49	7.72	124	97.04	4.44	44	97.35	3.58	36	97.51	3.40
Niger	445	99.68	1.55	112	99.68	1.07	43	99.66	0.56	37	99.69	0.57
North Korea	242	99.84	1.44	79	99.74	1.49	33	99.74	1.23	29	99.74	1.29
Northern Cyprus	103	99.14	1.69	50	99.11	1.45	27	99.03	1.36	21	99.16	1.46
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	99.82	0.56	21	99.87	0.34	12	99.90	0.27	9	99.86	0.31
Palestina	207	98.86	2.56	78	98.83	1.83	33	98.59	2.38	27	98.71	2.47
Papua New Guinea	839	99.98	1.62	99	99.98	1.00	37	99.86	1.06	30	99.79	1.17
Paraguay	818	96.58	8.78	116	96.07	6.36	44	96.85	3.76	36	96.87	4.09
Puerto Rico	145	98.81	4.48	56	98.80	4.37	29	98.52	4.17	23	98.32	4.64
Republic of Congo	747	100.05	4.29	131	100.04	2.21	47	100.24	1.80	38	100.12	1.61
Reunion	17	99.39	1.29	13	99.22	1.09	7	98.96	1.13	7	98.96	1.13
Saint Kitts and Nevis	40	100.07	0.56	22	100.13	0.47	12	100.05	0.36	9	100.04	0.39
Saint Lucia	49	99.83	0.46	29	99.80	0.45	13	99.85	0.22	9	99.86	0.13
Saint-Barthelèmy	19	100.13	0.26	13	100.08	0.20	9	100.09	0.17	6	100.08	0.18
Saint-Martin	23	99.87	1.87	16	99.68	1.56	11	99.55	1.45	7	100.10	1.32
Samoa	16	100.00	0.00	13	100.00	0.00	7	100.00	0.00	7	100.00	0.00
San Marino	45	99.56	2.93	26	99.46	2.37	14	98.86	2.79	10	99.19	2.50
Senegal	534	100.20	1.19	121	100.20	0.83	46	100.23	0.68	39	100.21	0.66
Seychelles	31	100.20	0.24	19	100.16	0.25	12	100.18	0.27	10	100.20	0.29
Sierra Leone	596	99.57	2.15	124	99.57	1.35	46	99.53	0.80	38	99.48	0.85
Sint Maarten	24	98.64	4.20	16	98.23	3.96	11	97.59	3.10	7	98.59	2.62
Solomon Islands	172	99.49	1.54	50	99.72	0.63	25	99.75	0.45	20	99.70	0.48
Somalia	633	99.81	1.18	133	99.85	0.68	47	99.84	0.64	40	99.85	0.68
South Sudan	893	101.07	2.63	138	101.06	1.51	49	100.83	1.01	40	101.03	0.91
St. Vincent & the Grenadines	50	99.85	0.28	30	99.89	0.19	15	99.90	0.14	11	99.89	0.14
Sudan	598	100.32	2.24	124	100.28	1.06	45	100.21	0.89	39	100.29	0.82
Suriname	855	100.00	2.53	123	99.81	2.11	44	99.76	1.62	36	99.69	1.74

Table A.4: 2012 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
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	99.24	2.92	130	98.96	2.04	47	98.70	1.96	37	98.83	2.11
Syria	285	99.96	1.07	88	99.83	0.90	36	99.78	1.21	30	99.74	1.33
São Tomé and Príncipe	50	99.87	1.48	33	100.03	0.30	16	100.00	0.21	14	99.99	0.22
Tajikistan	240	99.96	0.95	73	99.98	0.66	31	99.90	0.55	26	99.92	0.59
Tanzania	1228	99.85	1.59	150	99.81	0.57	53	99.81	0.38	44	99.78	0.38
Timor-Leste	175	99.68	2.81	68	99.75	2.20	31	99.44	3.19	27	99.35	3.41
Togo	610	100.04	3.03	122	100.11	2.08	45	100.24	1.50	37	100.20	1.39
Turkmenistan	255	100.62	2.21	74	100.60	1.33	32	100.58	0.94	27	100.68	0.94
Turks and Caicos Islands	52	99.85	0.25	29	99.92	0.25	17	99.94	0.20	13	99.95	0.20
Uganda	1122	99.93	1.42	141	99.84	1.20	50	99.93	0.50	42	99.98	0.37
Uzbekistan	260	99.10	5.92	78	99.08	3.75	33	99.49	2.22	28	99.49	2.41
Vanuatu	53	103.48	12.73	24	101.32	14.47	15	98.52	16.90	14	98.35	17.52
Virgin Islands, U.S.	58	97.86	4.39	33	97.77	4.21	23	97.67	3.99	19	97.82	3.14
Western Sahara	78	100.00	0.02	35	100.00	0.01	19	100.00	0.01	14	100.00	0.01
Yemen	230	99.84	3.05	76	100.01	0.95	30	99.95	0.70	25	100.00	0.60
Zimbabwe	739	99.73	1.12	138	99.74	0.65	50	99.72	0.59	41	99.77	0.60
Åland	55	100.37	1.54	31	100.35	0.89	17	100.27	0.97	15	100.24	1.01

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 2012 for each country excluded from the final regression sample.

Table A.5: 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
Azerbaijan	313	99.85	1.30	80	99.78	0.75	36	99.75	0.76	29	99.81	0.76
Bahrain	29	93.50	13.86	20	94.03	13.69	12	92.38	10.72	10	93.03	11.64
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
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
Bolivia	1690	98.30	5.04	143	98.35	3.44	47	98.86	2.99	38	99.00	3.22
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
Cameroon	1039	98.51	4.53	144	98.37	4.57	50	98.62	2.31	41	98.94	1.83
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

Table A.5: 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
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
Estonia	191	99.92	5.99	64	100.43	3.79	30	100.42	4.21	26	100.62	4.49
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
Hungary	242	99.58	2.49	69	99.57	1.30	33	99.51	1.54	28	99.55	1.64
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
Iraq	301	100.25	1.95	82	100.32	1.26	34	100.23	1.02	28	100.37	1.03
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
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
Latvia	197	99.41	5.91	65	100.09	3.20	30	99.99	3.79	26	100.08	4.07
Lebanon	212	99.48	1.83	78	99.31	1.45	32	99.34	1.49	26	99.40	1.61
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
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
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
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
Qatar	46	100.82	5.40	28	101.54	6.26	17	102.76	7.70	13	103.74	8.62
Romania	288	99.23	1.43	79	99.18	1.04	35	99.19	1.03	30	99.14	1.06
Russia	643	99.75	2.90	110	99.77	1.51	39	100.00	1.71	32	99.79	1.18
Rwanda	762	100.75	3.37	124	101.04	2.43	46	100.80	2.07	38	101.07	1.77
Saudi Arabia	239	100.55	3.62	80	100.37	1.92	32	100.48	1.93	26	100.65	2.09
Serbia	272	99.45	1.56	74	99.45	0.99	33	99.42	0.98	28	99.42	1.02

Table A.5: 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
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
Slovenia	260	99.59	2.02	74	99.68	1.57	34	99.60	1.49	29	99.45	1.12
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
Taiwan	378	97.89	2.55	97	97.79	2.19	34	97.67	1.63	28	97.62	1.62
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
Zambia	829	99.79	2.12	139	99.66	1.64	50	99.86	1.18	41	100.05	0.62

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.6: 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
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
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
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
Cape Verde	15	99.97	0.93	10	99.99	0.72	7	100.02	0.80	7	100.02	0.80

Table A.6: 2021 Area Score by Taxonomic Classification and Country, Out-of-Sample

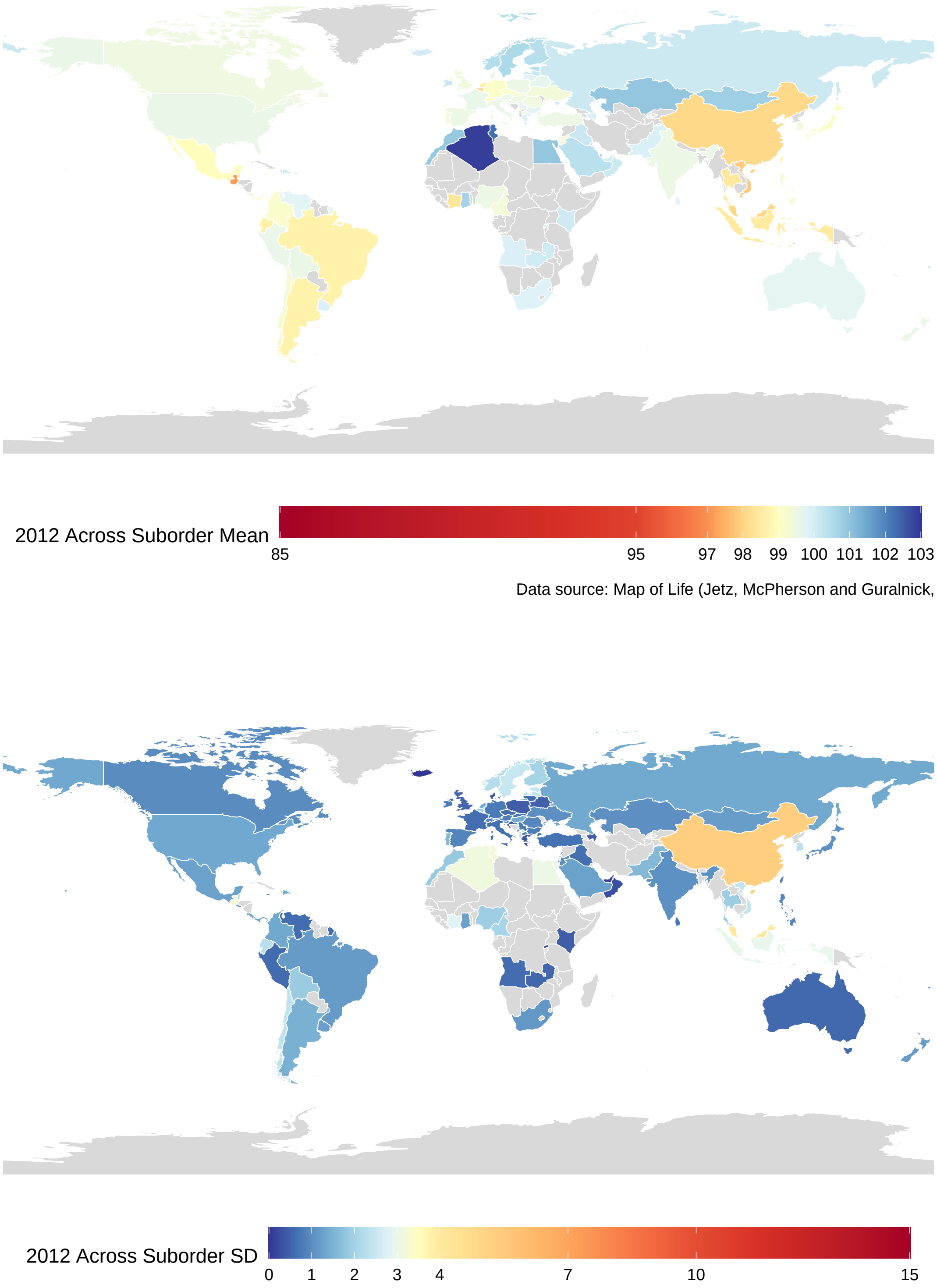
	Species			**Family**			**Suborder**			**Order**		
Country	Count	Mean	SD	Count	Mean	SD	Count	Mean	SD	Count	Mean	SD
Cayman Islands	48	99.60	5.00	24	99.61	3.56	14	100.25	4.56	11	99.62	3.12
Central African Republic	815	99.48	2.32	135	99.60	1.31	50	99.61	1.01	41	99.70	0.94
Chad	539	99.93	3.20	119	100.03	2.12	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
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
Iran	506	100.91	4.01	100	101.05	2.10	37	101.25	1.97	31	101.53	1.96
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
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
Lesotho	370	99.50	1.53	109	99.54	1.03	44	99.46	1.16	35	99.70	0.83
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
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

Table A.6: 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
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
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
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
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
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
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
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
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.

Figure B.2: 2012 Across Suborder Mean and Standard Deviation by Country

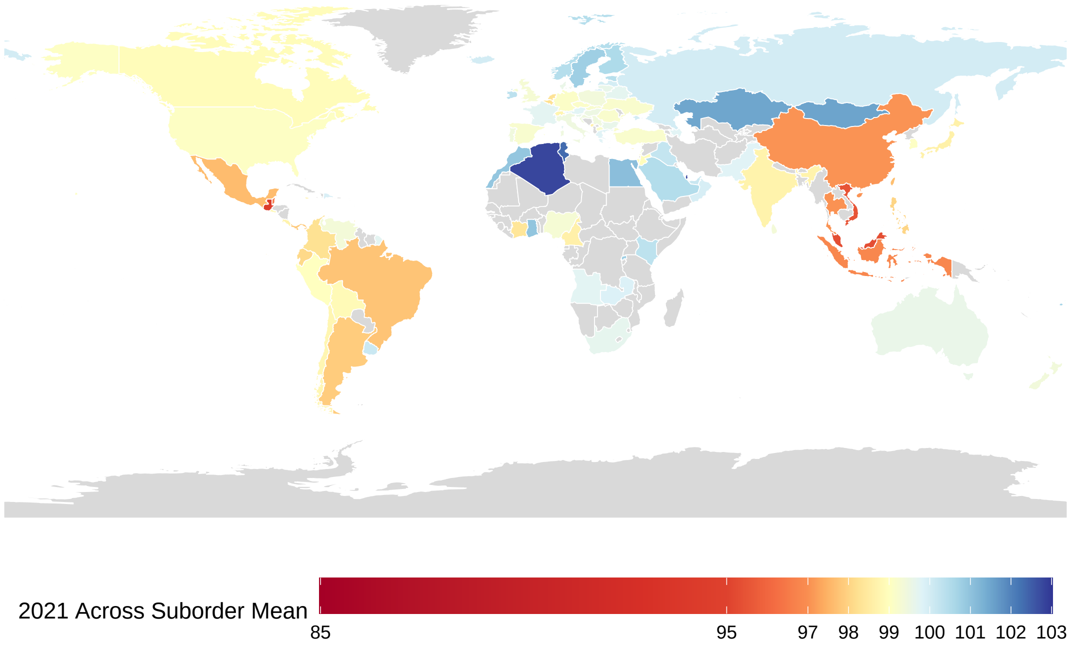


Data source: Map of Life (Jetz, McPherson and Guralnick, 2012)

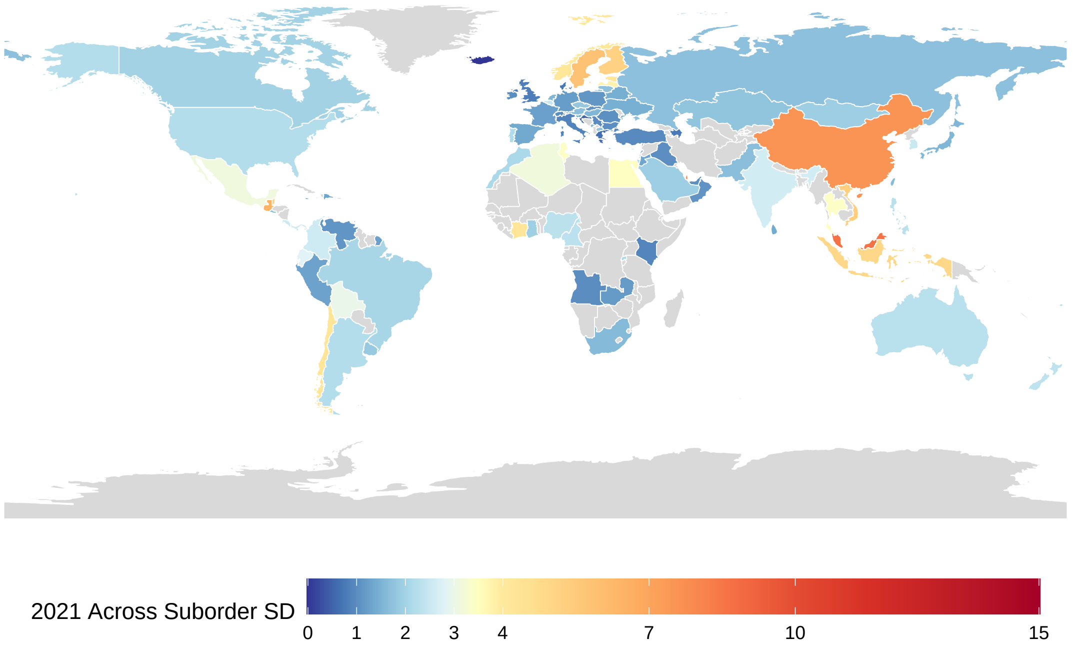
Data source: Map of Life (Jetz, McPherson and Guralnick, 2012)

Note: This map shows the across-order mean and standard deviation of area scores in 2012 for each country in our final regression sample.

Figure B.3: 2021 Across Suborder Mean and Standard Deviation by Country



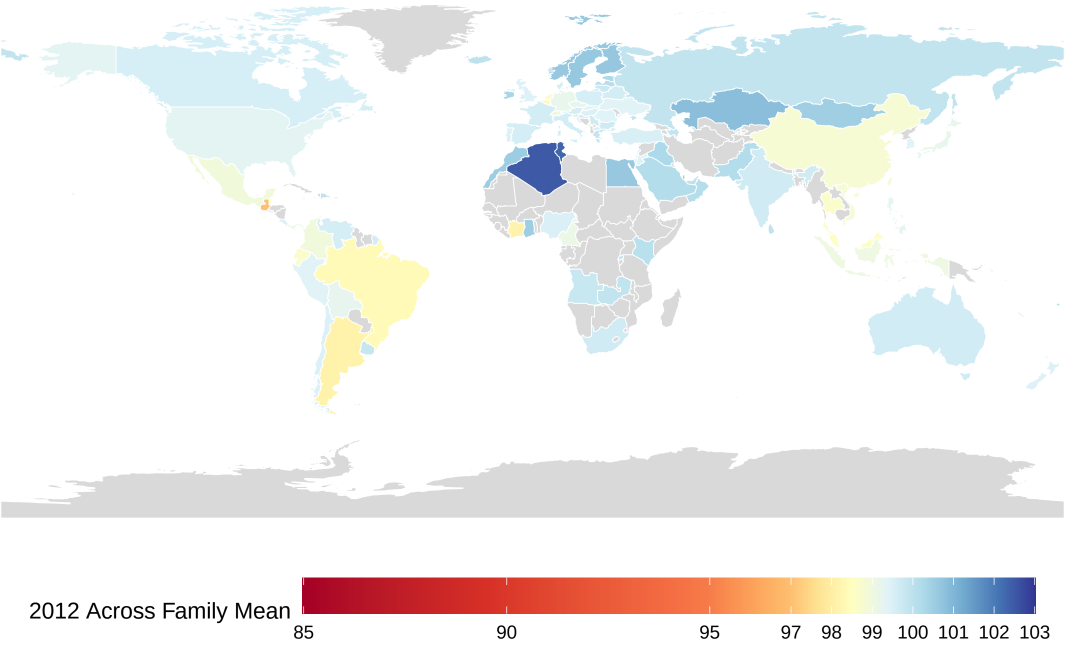
Data source: Map of Life (Jetz, McPherson and Guralnick, 2012)



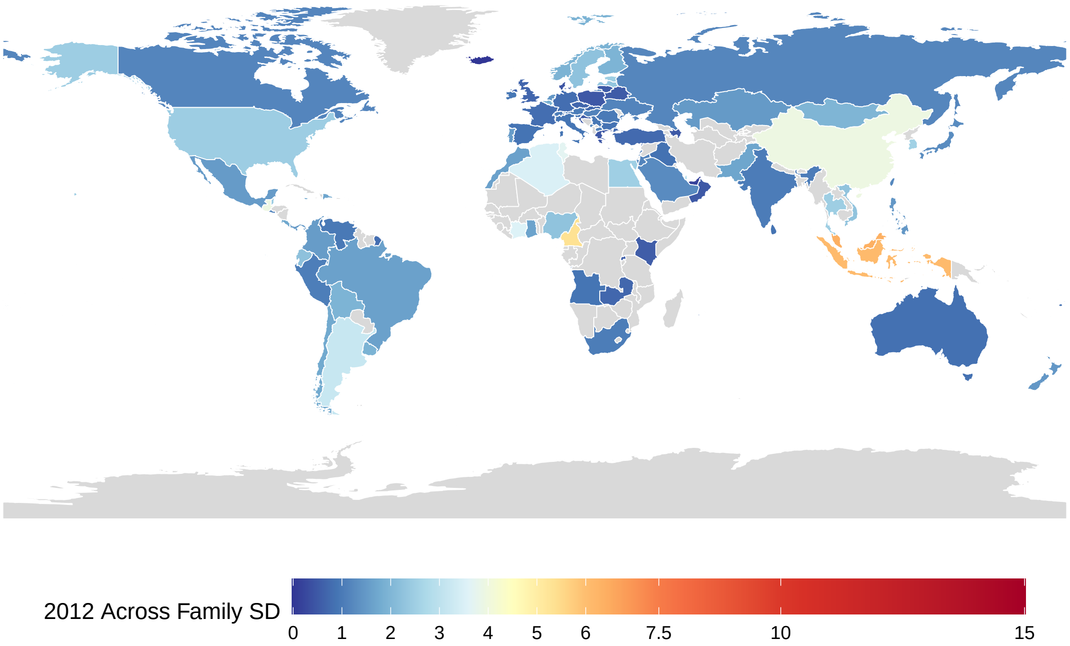
Data source: Map of Life (Jetz, McPherson and Guralnick, 2012)

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

Figure B.4: 2012 Across Family Mean and Standard Deviation by Country



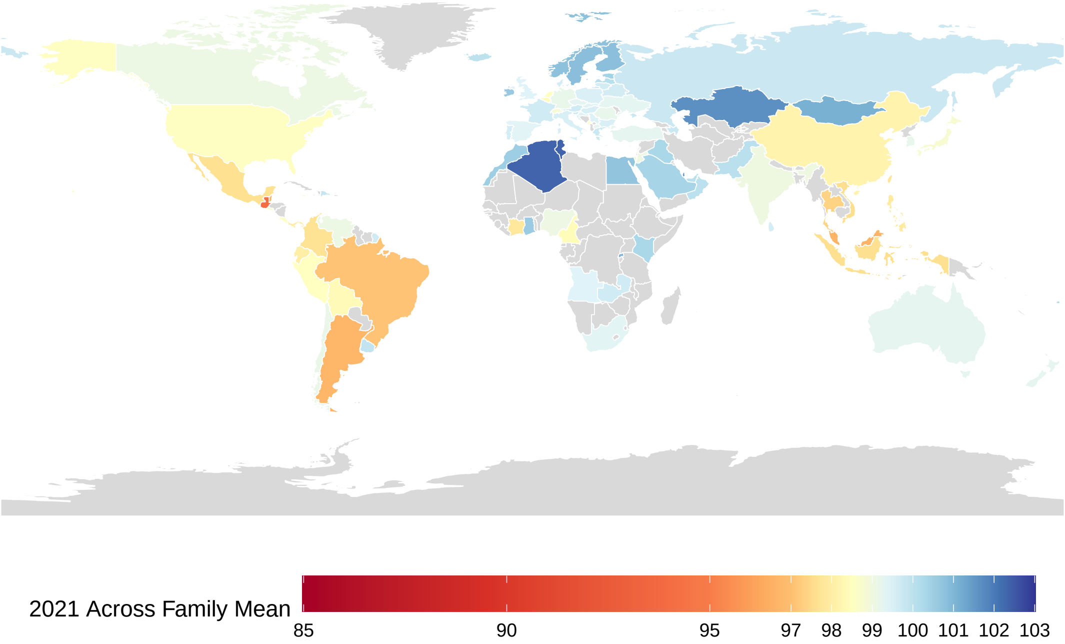
Data source: Map of Life (Jetz, McPherson and Guralnick, 2012)



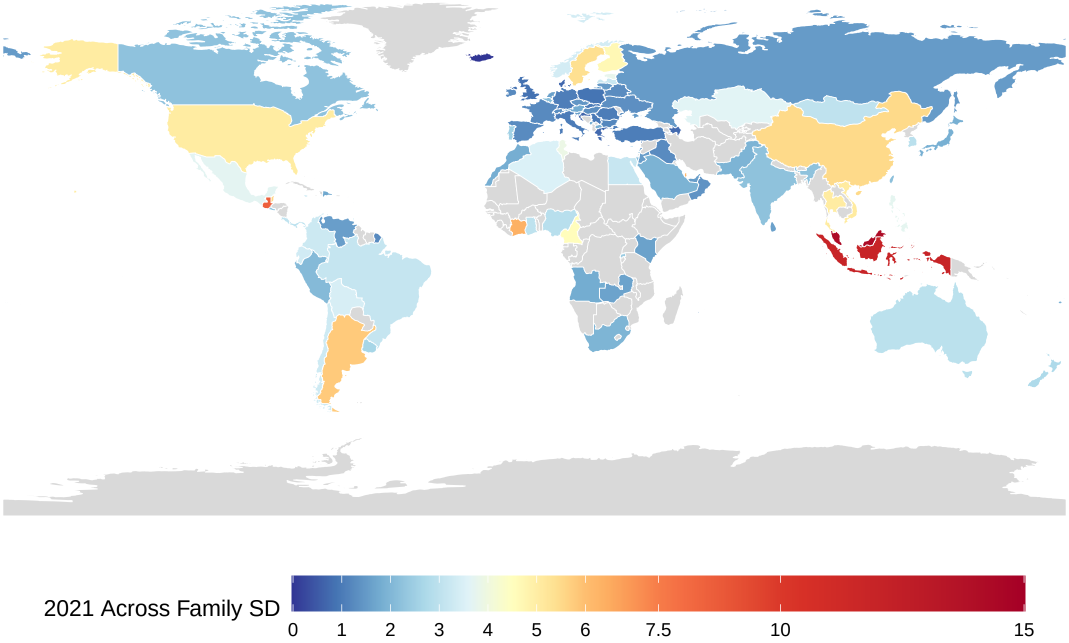
Data source: Map of Life (Jetz, McPherson and Guralnick, 2012)

Note: This map shows the across-family mean and standard deviation of area scores in 2012 for each country in our final regression sample.

Figure B.5: 2021 Across Family Mean and Standard Deviation by Country



Data source: Map of Life (Jetz, McPherson and Guralnick, 2012)



Data source: Map of Life (Jetz, McPherson and Guralnick, 2012)

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

Table A.7: Correlation between Measures of Imbalance in Habitat Destruction

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)
(1) Across-Suborder SD in 2012	1.00											
(2) Across-Suborder p10 in 2012	0.85	1.00										
(3) Across-Suborder Min in 2012	0.81	0.77	1.00									
(4) Across-Suborder SD in 2021	0.80	0.66	0.60	1.00								
(5) Across-Suborder p10 in 2021	0.73	0.86	0.69	0.80	1.00							
(6) Across-Suborder Min in 2021	0.63	0.65	0.79	0.74	0.79	1.00						
(7) Across-Family SD in 2012	0.92	0.78	0.74	0.79	0.71	0.63	1.00					
(8) Across-Family p10 in 2012	0.64	0.80	0.65	0.60	0.80	0.64	0.70	1.00				
(9) Across-Family Min in 2012	0.59	0.53	0.77	0.43	0.51	0.60	0.70	0.52	1.00			
(10) Across-Family SD in 2021	0.51	0.42	0.37	0.70	0.55	0.51	0.68	0.46	0.37	1.00		
(11) Across-Family p10 in 2021	0.52	0.65	0.56	0.71	0.87	0.73	0.62	0.88	0.48	0.55	1.00	
(12) Across-Family Min in 2021	0.46	0.46	0.60	0.58	0.61	0.79	0.58	0.52	0.74	0.53	0.65	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 (suborder and family) and two years (2012 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).

Table A.8: Spearman Rank Correlation between Measures of Imbalance in Habitat Destruction

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)
(1) Across-Suborder SD in 2012	1.00											
(2) Across-Suborder p10 in 2012	0.68	1.00										
(3) Across-Suborder Min in 2012	0.74	0.79	1.00									
(4) Across-Suborder SD in 2021	0.79	0.61	0.61	1.00								
(5) Across-Suborder p10 in 2021	0.58	0.85	0.68	0.72	1.00							
(6) Across-Suborder Min in 2021	0.58	0.66	0.79	0.76	0.77	1.00						
(7) Across-Family SD in 2012	0.93	0.67	0.73	0.78	0.58	0.60	1.00					
(8) Across-Family p10 in 2012	0.69	0.96	0.79	0.62	0.81	0.67	0.70	1.00				
(9) Across-Family Min in 2012	0.66	0.64	0.85	0.55	0.55	0.68	0.75	0.67	1.00			
(10) Across-Family SD in 2021	0.73	0.58	0.59	0.94	0.69	0.73	0.81	0.60	0.63	1.00		
(11) Across-Family p10 in 2021	0.58	0.83	0.68	0.74	0.96	0.77	0.62	0.85	0.60	0.74	1.00	
(12) Across-Family Min in 2021	0.53	0.56	0.70	0.69	0.65	0.86	0.62	0.60	0.81	0.78	0.71	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 (suborder and family) and two years (2012 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).

Table A.9: Summary Statistics

	Mean	SD	p5	p25	p50	p75	p95
Regression Sample (N=886,807)							
CDS spread level (bps)	212.31	306.37	6.86	40.47	119.70	268.50	703.95
Absolute Change in CDS spread level (weekly, bps)	0.165	20.266	-23.156	-2.910	-0.000	2.319	23.776
% Change in CDS spread (weekly)	0.428	9.298	-12.423	-2.978	-0.000	2.593	15.274
Tenor							
1Y (as % of sample)	17.8						
5Y (as % of sample)	18.8						
10Y (as % of sample)	18.1						
15Y (as % of sample)	15.1						
20Y (as % of sample)	15.4						
30Y (as % of sample)	14.9						
Biodiversity News (standardized)	0.013	1.027	-1.343	-0.794	0.020	0.547	1.801
Biodiversity Destruction Score in 2012 (standardized)	0.118	0.944	-2.760	-0.248	0.403	0.689	1.209
Across-Suborder Dispersion of Habitat Destruction in 2012 (standardized)	-0.030	0.845	-0.850	-0.605	-0.253	0.316	1.416
Biodiversity - Country Level (N=99)							
Biodiversity Destruction Score in 2012	66.61	11.33	33.17	62.78	69.08	73.84	80.29
Biodiversity Destruction Score in 2022	68.88	13.02	33.17	66.67	72.40	76.71	83.61
Biodiversity Destruction Score in 2012 (standardized)	-0.000	1.000	-2.952	-0.338	0.219	0.638	1.207
Dispersion of Habitat Destruction - Country Level (N=79)							
Across-Suborder Dispersion of Habitat Destruction in 2012	1.506	1.287	0.376	0.686	1.182	1.949	4.074
Across-Suborder Dispersion of Habitat Destruction in 2012 (standardized)	0.000	1.000	-0.878	-0.637	-0.253	0.344	1.995

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 3.3 and section B. “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 (standardized)” are the standardized 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 2012 and 2022. “Across-Suborder Dispersion of Habitat Destruction” is the across-suborder standard deviation of average habitat loss by suborder. We standardize the “Biodiversity News”, “Biodiversity Destruction Score” and “Across-Suborder 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.10: Correlation Between Measures of Biodiversity Reliance and Degradation

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
(1) Biodiversity Destruction Score-2012	1.00									
(2) Biodiversity Destruction Score-2022	0.71	1.00								
(3) Biodiversity Destruction Score-Avg	0.91	0.94	1.00							
(4) Biodiversity Destruction Score (No Ecosystem)-2012	0.43	0.31	0.40	1.00						
(5) Environmental Vulnerability Index	0.14	-0.01	0.07	0.46	1.00					
(6) Across-Suborder Dispersion of Area Scores in 2012	-0.12	0.00	-0.06	-0.25	0.14	1.00				
(7) Across-Suborder Dispersion of Area Scores in 2021	-0.15	0.03	-0.06	-0.31	0.05	0.92	1.00			
(8) Across-Family Dispersion of Area Scores in 2012	-0.07	0.02	-0.02	-0.24	0.07	0.91	0.87	1.00		
(9) Across-Family Dispersion of Area Scores in 2021	-0.06	0.05	-0.00	-0.26	-0.01	0.82	0.90	0.93	1.00	
(10) Across-Suborder Dispersion of Habitat Scores in 2012	-0.08	0.02	-0.03	-0.10	-0.17	0.26	0.18	0.26	0.21	1.00

Note: The table shows the correlation between our measures of biodiversity reliance and degradation. "Biodiversity Destruction Score" includes indicators for the change 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 shown for 2012, 2022, and the average of these two values. "Biodiversity Destruction Score (No Ecosystem)-2012" 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, in 2012. 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-Suborder Dispersion of Area Scores" is the across-suborder standard deviation of within-suborder average species area scores, provided by the Map of Life (Jetz, McPherson and Guralnick, 2012). The "Across-Family Dispersion of Area Scores" uses the standard deviation across family instead, and values for these area scores are shown for 2012 and 2021. The "Across-Suborder Dispersion of Habitat Scores" follows the same method but applies habitat scores, also provided by the Map of Life, and is shown for 2012.

Table A.11: CDS Spreads Reaction to Biodiversity News - Robustness

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
Biodiversity News	0.192	0.147	0.175	0.188	0.191	0.190	0.191	0.189
	(0.137)	(0.119)	(0.129)	(0.138)	(0.138)	(0.138)	(0.138)	(0.138)
Biodiversity News ×	0.073^{**}	0.065^{**}	0.068^{**}	0.072^{**}	0.063^{**}	0.060^{**}	0.043^{*}	0.062^{**}
Measure of Mean Biodiversity Destruction	(0.029)	(0.026)	(0.029)	(0.029)	(0.027)	(0.027)	(0.026)	(0.029)
Biodiversity News ×	0.051^{**}	0.041^{**}	0.052^{**}	0.035	0.069^{**}	0.052^{***}	0.039^{*}	0.044^{**}
Vulnerable Group Habitat Destruction Metric	(0.020)	(0.019)	(0.022)	(0.022)	(0.029)	(0.008)	(0.020)	(0.021)
Country × Year × Tenor × Currency FE	x	x	x	x	x	x	x	x
Specification Variant	No Inno	Win 2%	USD only					
Dispersion Measure Variant				2021	p10	min		
Mean Destruction Score Variant							2021	Avg
Observations	865,169	865,169	464,663	865,169	865,169	865,169	865,169	865,169

Note: This table presents robustness checks for Table 1. The baseline specification from column 2 of Table 1 regresses percent changes in CDS spreads, winsorized at the 1st and 99th percentile, on AR(1) innovations of the *Biodiversity News* index by Giglio et al. (2023), as well as the interactions of innovations in biodiversity news with two measures: our *Biodiversity Destruction Score* and *Across-Suborder Dispersion of Area Scores*, in 2012. All regressions include country-year-tenor-currency fixed effects. Regression (1) modifies the baseline specification by regressing on the *Biodiversity News* index directly. Regression (2) winsorizes percent changes in CDS spreads at the 2nd and 98th percentile. Regression (3) restricts the sample to USD-denominated CDS. Regression (4) uses 2021 value of the *Across Suborder Dispersion of Area Scores*, while Regression (5) replaces the standard deviation of area scores across suborders with the 10th percentile value, and Regression (6) uses the minimum value of area scores across families. Regression (7) uses the 2022 value of the *Biodiversity Destruction Score*, while Regression 8 uses the average of the 2012 and 2022 values. For all measures, higher scores indicate greater mean and dispersion of biodiversity degradation. Standard errors are in parentheses and are double-clustered at the country-month level. Significance levels: * ($p<0.10$), ** ($p<0.05$), *** ($p<0.01$).

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.[27] 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 Calibration of Elasticity of Substitution σ

We illustrate how to calibrate the elasticity of substitution σ between ecosystem functions, using the empirical findings from Sutter and Albrecht (2016) as an example. 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, holding other functions $g \neq 1, 2$ at $E_g = \bar{E}$. Denote

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[27] 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.

$$\mathcal{E}\left(E_1, E_2, \sigma\right) = \left[E_1^{\frac{\sigma-1}{\sigma}} + E_2^{\frac{\sigma-1}{\sigma}} + \sum_{g \neq 1,2} \bar{E}^{\frac{\sigma-1}{\sigma}}\right]^{\frac{\sigma}{\sigma-1}}$$

We can then define

$$\begin{aligned}
\text{Single effect 1} &= \frac{\mathcal{E}(\bar{E}(1+\Delta_1), \bar{E}, \sigma) - \mathcal{E}(\bar{E}, \bar{E}, \sigma)}{\mathcal{E}(\bar{E}, \bar{E}, \sigma)} = \frac{\mathcal{E}(1+\Delta_1, 1, \sigma) - \mathcal{E}(1,1,\sigma)}{\mathcal{E}(1,1,\sigma)} \\
\text{Single effect 2} &= \frac{\mathcal{E}(\bar{E}, \bar{E}(1+\Delta_2), \sigma) - \mathcal{E}(\bar{E}, \bar{E}, \sigma)}{\mathcal{E}(\bar{E}, \bar{E}, \sigma)} = \frac{\mathcal{E}(1, 1+\Delta_2, \sigma) - \mathcal{E}(1,1,\sigma)}{\mathcal{E}(1,1,\sigma)} \\
\text{Joint effect} &= \frac{\mathcal{E}(\bar{E}(1+\Delta_1), \bar{E}(1+\Delta_2), \sigma) - \mathcal{E}(\bar{E}, \bar{E}, \bar{E})}{\mathcal{E}(\bar{E}, \bar{E}, \sigma)} = \frac{\mathcal{E}(1+\Delta_1, 1+\Delta_2, \sigma) - \mathcal{E}(1,1,\sigma)}{\mathcal{E}(1,1,\sigma)}
\end{aligned}$$

where the second equality in each line follows from the fact that the CES aggregator is homogeneous of degree 1. In general, using estimates for these three effects allows us to solve a system of three equations in three unknowns $(\Delta_1, \Delta_2, \sigma)$. Given how close the two estimated single effects are (6% and 7%), we assume a symmetric improvement $\Delta_1 = \Delta_2 = \Delta$ leading to a single effect equal to about 6.5% and a joint effect of 23% increase in total ecosystem services. Therefore, in this example, σ is such that

$$\frac{\mathcal{E}(1+\Delta, 1, \sigma)}{\mathcal{E}(1+\Delta, 1+\Delta, \sigma)} = \frac{1.065}{1.23}.$$

which corresponds to $\sigma \approx 0.1$.

C.3 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 and uncertain species loss. 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, defined for each species i irrespectively of the expected distance to other surviving species j (in Weitzman's analogy, species are libraries that house collections of genes as books, and U_i "*represents how much the library building itself is liked irrespective of its book content*"), and its *distinctiveness* D_i that captures how unique it is expected to be relative to other surviving 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).

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 $U_{i,g} = \log \frac{a_g \alpha_g \bar{E}_g}{s_g^{1-\alpha_g} \bar{S}_g}$ and allows us 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 it sharpens differences between functions that have experienced differential losses; for similar reasons, it increases distinctiveness more for species in functions with low s_g and low substitutability ϵ_g.

C.4 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 and 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.[28]

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:

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

This trend in expected fragility 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 $\sum_{g=1}^{G}\omega_g\frac{1}{s_g(\epsilon_g-1)}$, 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 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.

We can also 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:

$$\begin{aligned}\mathrm{BR}(t) &= \frac{1}{\delta}\sqrt{\mathbb{E}_0\left[\mathrm{Var}(d\log E(t))\right]} && \text{(A.1)}\\ &= \sqrt{\mathbb{E}_0\left[\mathrm{Var}(\mathcal{F}(\boldsymbol{s}(t)))\right]} && \text{(A.2)}\end{aligned}$$

The increased fragility translates into an increasing expected range of potential effects on ecosystem service provision from a given species loss, as measured by 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 $\mathrm{BR}(t)$ as defined in equation (A.2) 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

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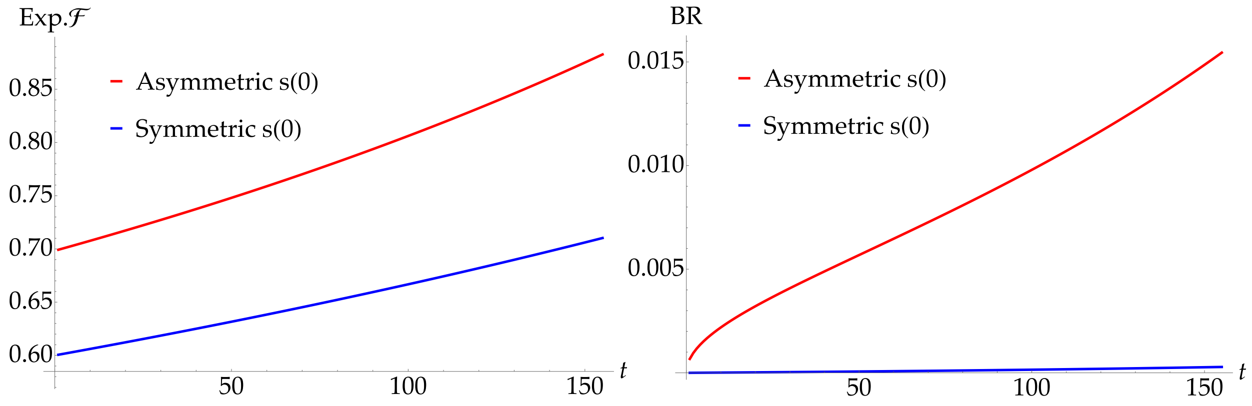
[28] In this specification, δ is the per-period average species loss expressed as a share of the maximal number of species $\bar{S}$ (e.g., $\delta = 1/\bar{S}$ corresponds to losing one species per period). Community abundance declines deterministically as $N(t) = N(0) - \delta t$.

Figure C.6: 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: $\sigma = 0.5$, $\phi = 0.3$, $\mu = 1/1000$.

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.6 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.

C.5 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.6 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 $\sigma > 0$

$$1 - u^* = \left[s_0 - \delta\left(1 + \Lambda(1+\phi)\right)\right] \frac{\sqrt{1 + \frac{4\Lambda\delta(s_0-\delta)}{[s_0-\delta(1+\Lambda(1+\phi))]^2}} - 1}{2\delta}. \tag{A.3}$$

C.7 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 A.1. *The vector of optimal conservation across functions satisfies*

$$\frac{1}{\sum_g \frac{\mu_g(\boldsymbol{s}_1)}{1-u_g}} = \frac{\Lambda}{1 - \Lambda\delta\mathcal{F}(\boldsymbol{s}_1)}. \tag{A.4}$$

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.4) is the counterpart of equation (27) in Proposition 3, but replacing the uniform land use u with the harmonic weighted-average of optimal conservation levels across functions $(\sum_g \mu_g(\boldsymbol{s}_1)/(1-u_g))^{-1}$, 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 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 toward 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.8 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

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

C.9 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

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

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

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

D 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

$$E_{-g} = \left(\sum_{j \neq g} E_j^{\frac{\sigma-1}{\sigma}} \right)^{\frac{\sigma}{\sigma-1}}, \tag{A.5}$$

so that

$$E = \left[E_g^{\frac{\sigma-1}{\sigma}} + E_{-g}^{\frac{\sigma-1}{\sigma}} \right]^{\frac{\sigma}{\sigma-1}}. \tag{A.6}$$

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:

$$\frac{\partial E}{\partial S_g} = \phi_g \frac{\bar{E}_g^{\frac{\sigma-1}{\sigma}}}{\bar{S}_g} s_g^{\phi_g \frac{\sigma-1}{\sigma} - 1} \left[\bar{E}_g^{\frac{\sigma-1}{\sigma}} s_g^{\phi_g \frac{\sigma-1}{\sigma}} + E_{-g}^{\frac{\sigma-1}{\sigma}} \right]^{\frac{1}{\sigma-1}} \tag{A.7}$$

$$\frac{\partial^2 E}{\partial S_g^2} = - \frac{\bar{E}_g \phi_g Z_{-g}^{\frac{1}{\sigma}} s_g^{\phi_g} \left(\left(\bar{E}_g s_g^{\phi_g} \right)^{\frac{\sigma-1}{\sigma}} + Z_{-g}^{\frac{\sigma-1}{\sigma}} \right)^{\frac{\sigma}{\sigma-1}}}{\sigma S_g^2 \left(\bar{E}_g Z_{-g}^{\frac{1}{\sigma}} s_g^{\phi_g} + Z_{-g} \left(\bar{E}_g s_g^{\phi_g} \right)^{\frac{1}{\sigma}} \right)^2} \left[\bar{E}_g \sigma (1 - \phi_g) Z_{-g}^{\frac{1}{\sigma}} s_g^{\phi_g} + Z_{-g} (\sigma(1 - \phi_g) + \phi_g) \left(\bar{E}_g s_g^{\phi_g} \right)^{\frac{1}{\sigma}} \right] \tag{A.8}$$

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 $s_g^{\phi_g \frac{\sigma-1}{\sigma}}$ 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.7):

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

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 $\mathrm{Cov}(x,y) = \sum_g (x_g - \frac{1}{G}\sum_j x_j)(y_g - \frac{1}{G}\sum_j y_j)$. 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 $\sum_g f_g(\boldsymbol{s},\boldsymbol{\theta}) = 1$.

As noted in Section 2, we focus on shocks $\boldsymbol{ds}$ in Proposition 2 but prove a more general result that also allows for shocks to abundance holding biodiversity fixed, that is, shocks $\boldsymbol{d\bar{n}} = \{d\bar{n}_g\}_g$.

The sum of community abundances across functions is

$$N = \sum_{g=1}^G \bar{n}_g \bar{S}_g s_g^{\alpha_g}$$

hence

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

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

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

Defining the abundance weights as in the Proposition,

$$\omega_g = f_g(\boldsymbol{s},\boldsymbol{\alpha}) = \frac{s_g^{\alpha_g}}{\sum_{j=1}^G s_j^{\alpha_j}}$$

this rewrites

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

We next turn to aggregate ecosystem services

$$E = \left[\sum_{g=1}^G \left(\bar{S}_g \bar{n}_g\right)^{\frac{\sigma-1}{\sigma}} s_g^{\phi_g \frac{\sigma-1}{\sigma}}\right]^{\sigma/\sigma-1}.$$

Define the criticality weights as in the Proposition

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

and the criticality-abundance gaps

$$\gamma_g = \mu_g - \omega_g.$$

Then the shocks $\boldsymbol{ds}$ and $\boldsymbol{d\bar{n}}$ have the following first-order effect on aggregate ecosystem services:

$$\begin{aligned}
d\log E &= \sum_{g=1}^{G} f_g\left(\boldsymbol{s}, \phi\frac{\sigma-1}{\sigma}\right)\left[\frac{d\bar{n}_g}{\bar{n}_g} + \frac{\phi_g}{s_g}ds_g\right] \\
&= \sum_{g=1}^{G}\left[\gamma_g + \omega_g\right]\left[\frac{d\bar{n}_g}{\bar{n}_g} + \frac{\phi_g}{s_g}ds_g\right] \\
&= \sum_{g=1}^{G}\omega_g\left[\frac{d\bar{n}_g}{\bar{n}_g} + \left(\phi_g - \alpha_g + \alpha_g\right)\frac{ds_g}{s_g}\right] + \sum_{g=1}^{G}\gamma_g\left[\frac{d\bar{n}_g}{\bar{n}_g} + \frac{\phi_g}{s_g}ds_g\right] \\
&= \underbrace{\sum_{g=1}^{G}\omega_g\left[\frac{d\bar{n}_g}{\bar{n}_g} + \frac{\alpha_g}{s_g}ds_g\right]}_{d\log N} + \sum_{g=1}^{G}\frac{\omega_g}{\epsilon_g - 1}\frac{ds_g}{s_g} + \sum_{g=1}^{G}\gamma_g\left[\frac{d\bar{n}_g}{\bar{n}_g} + \frac{\phi_g}{s_g}ds_g\right]
\end{aligned}$$

where we used $\sum_g \gamma_g = 0$ and $\phi_g - \alpha_g = \frac{1}{\epsilon_g - 1}$. This reduces to the simpler expression in Proposition 2 if we set $d\bar{n}_g = 0$ for all g.

Common shocks and fragility. Consider a common shock to all functions $ds_g = ds$, with no shock to $\boldsymbol{\bar{n}}$. Then

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

and

$$\begin{aligned}
d\log E &= \left[\sum_{g=1}^{G}\omega_g\frac{\phi_g}{s_g}\right]ds + \mathrm{Cov}\left[\gamma_g, \frac{\phi_g}{s_g}\right]ds \\
&= \mathcal{F}(\boldsymbol{s})ds
\end{aligned}$$

where we define fragility as

$$\mathcal{F}(\boldsymbol{s}) = \left[\sum_g \mu_g\frac{\phi_g}{s_g}\right].$$

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

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

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

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

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

$$1-u^* = \frac{\Lambda}{1-\Lambda\delta\mathcal{F}(\boldsymbol{s}_0-\delta u^*\mathbf{1})}. \tag{A.9}$$

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.9) 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):

$$\left[X_1^{\frac{1}{\xi}-1} + 1 + \beta\theta\right] X_1^{\frac{1}{\theta}} = \frac{\beta\theta\left(\bar{u}L\right)^{\frac{1-\theta}{\theta}}}{E_1(u)^{\frac{1}{\theta}}} F(K_0, uL, s_0) \tag{A.10}$$

$$1 - u = \frac{\Lambda(u, X_1)}{1 - \Lambda(u, X_1)\delta\mathcal{F}\left(\boldsymbol{s}_0 - \delta u \mathbf{1}\right)}, \tag{A.11}$$

where $X_1 = \frac{K_1^{\theta}(\bar{u}L)^{1-\theta}}{E_1}$. The left-hand side of (A.10) 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.10) to get X_1 increasing in u and K_0. Then, the right-hand side of the second equation (A.11) 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 A.1. 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

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

$$\begin{aligned}
\frac{\partial \log E_1}{\partial \log(1 - u_g)} &= \frac{\left[\bar{E}_{g,0}(1 - u_g) s_{g,1}(s_{g,0}, u_g)^{\phi_g} \right]^{\frac{\sigma-1}{\sigma}}}{\sum_j \left[\bar{E}_{j,0}(1 - u_j) \left[s_{j,1}(s_{j,0}, u_j) \right]^{\phi_j} \right]^{\frac{\sigma-1}{\sigma}}} \left\{ 1 + \phi_g \frac{\partial \log s_{g,1}}{\partial \log(1 - u_g)} \right\} \\
\frac{\partial \log E_1}{\partial \log(1 - u_g)} &= \mu_g \left\{ 1 + (1 - u_g) \frac{\phi_g}{s_{g,1}} \delta \right\}.
\end{aligned}$$

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

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

Appendix References

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