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, (ii) how critical the affected function is for overall ecosystem productivity, and (iii) the extent to which ecosystem services constrain economic output relative to other factors of production. We derive an expression for the fragility of ecosystems and economic output to further biodiversity loss, and decompose this fragility into within-function and across-function effects. Ecosystem fragility increases with both mean species losses as well as the imbalance of species losses across ecosystem functions. Consistent with the model, we show that empirical measures of biodiversity degradation and ecosystem fragility are reflected in market assessments of risk in the cross-section of countries, which we extract from the prices of credit default swaps. We conclude by embedding our model of ecosystem services production in an intertemporal planning problem and study optimal land use when land use raises output at the cost of reducing biodiversity.

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

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In 2019, the *Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services* (IPBES) sounded the alarm. In its *Global Assessment*, the independent body tasked with providing policymakers with scientific assessments about the state of nature concluded that biodiversity was declining faster than at any time in human history. Reviewing a vast academic literature, the IPBES found that the global rate of species extinction was at least 10–100 times larger than the base rate over the past 10 million years; it also showed that the rate of species loss was 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 economic and financial implications. For example, in June 2023, Frank Elderson, Vice-Chair of the Supervisory Board of the European Central Bank (ECB), wrote that "*destroying nature means destroying the economy,*" announcing that the ECB would "*address the cascading effects of nature degradation and climate change on the economy and financial stability.*" In an interview with the Financial Times (2023), he expanded on this view, highlighting that "*biodiversity belongs in that list of things that affect the economy,*" and arguing that "*this is not some kind of a flower power, tree-hugging exercise... this is core economics.*" Similarly, 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 biodiversity loss might significantly disrupt economic activity, there is a notable lack of research on the relationship between the two.[1] While a substantial literature has studied nature's contribution to economic growth, this is usually done by considering a monolithic stock of "natural capital" that enters the production function. These existing approaches are generally silent on how to aggregate the totality of nature into such a singular measure of natural capital. Indeed, by abstracting from the interactions between different species, these models have no role for bio*diversity*, and provide no framework for exploring how various species contribute to aggregate economic activity.[2]

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

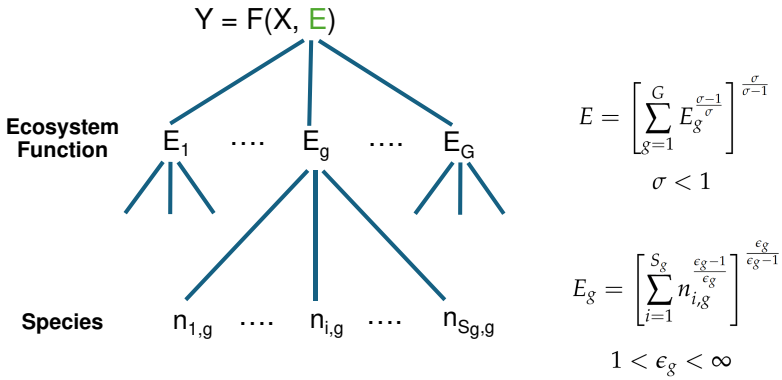
[1] This is in contrast to the more advanced work that integrates models of climate change and economic and financial activity (Nordhaus, 1991; Nordhaus and Boyer, 2003; Giglio, Kelly and Stroebel, 2021; Giglio et al., 2021; Barnett, Brock and Hansen, 2022; Barro, 2015; Weitzman, 2009). Similarly, work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

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

ecology literature but remains sufficiently tractable to be incorporated into 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. 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 Stiglitz, 1977). Consistent with insights from the ecology literature, different functions are complements in the production of aggregate ecosystem services (i.e., they have an elasticity of substitution $\sigma < 1$), capturing the idea that healthy and productive ecosystems are hard to sustain when key functions are missing and that a decline in the availability of one function cannot easily be compensated for by the growth of other functions (Sekercioglu, 2010; Fenichel, Dean and Schmitz, 2024; Potts et al., 2016).

At the bottom level, we model how different species interact to produce each specific ecosystem function. Here, 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 individuals in each species. Within this function-level aggregator, different species are highly substi-

tutable, 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 and more species are present. This means that 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 that perform a similar function in a species-rich ecosystem represents a form of diversification with respect to 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, a few remaining species may become "keystone species": species whose extinction will lead to large negative effects on ecosystem output and economic activity.

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 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.[3] Therefore, through the combination of the two hierarchical layers, each introducing a different source of concavity, our model can generate substantial (and realistic) non-linearities and tipping points that have been discussed in the ecology and biodiversity literature (e.g., Svartzman et al., 2021; Fenichel, Gopalakrishnan and Bayasgalan, 2015).

Having specified the hierarchical structure of our production function of ecosystem services, we characterize the aggregate impact of species losses across multiple functions. Specifically, we derive a decomposition reminiscent of 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 functions.

[3]The intuition for this is clearest in the case of extreme complementarity, where the CES aggregator collapses to a Leontief function in which the overall level of ecosystem service provision is given by the 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.

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 as well as 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 uses ecosystem services as complements to other factors of production, such as land and capital, to capture the idea that it is hard to substitute for the loss of ecosystem services through an increased use of other factors (Cohen, Hepburn and Teytelboym, 2019; Dasgupta, 2021). The relationship between biodiversity loss and economic output inherits many of the properties of the relationship between biodiversity loss and the production of aggregate ecosystem services. The complementarity between factors of production further amplifies the concavity of the relationship between biodiversity and ecosystem services: 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 and conduct a systematic empirical analysis. Given our emphasis on the aggregate effects of biodiversity loss, this work focuses on a cross-country analysis.[4] A systematic study of the macroeconomic effects of biodiversity loss is complicated by two factors. First, such effects tend to manifest over long horizons and at low frequencies. And second, as long as the current state of biodiversity is not too degraded, our model suggests that biodiversity loss should largely increase the risks from future biodiversity losses (through raising ecosystem fragility) without having large effects on current macroeconomic aggregates. For these reasons, we focus our analysis on 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*.

We do so by studying 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.

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

We then exploit the *cross-sectional* variation in biodiversity risk exposures across countries to provide evidence for several key predictions from our model. First, we show that negative biodiversity news induces significant increases in CDS spreads specifically for those countries with more depleted ecosystems as captured by several distinct indicators of average ecosystem health. Second, we show that *imbalances* in past biodiversity losses across functions additionally increase a country's biodiversity risk exposure. To test this prediction, we join data from the Map of Life project (Jetz, McPherson and Guralnick, 2012), 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 empirical analysis shows that, indeed, countries with a larger *dispersion* in species losses across functions experience larger increases in CDS spreads in response to negative biodiversity news. Third, we find that CDS spreads increase more upon negative biodiversity news in countries where ecosystem services are more likely to be a bottleneck in the production process.

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 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 particular, while ecosystem services and production can vary by geography, we model the production without explicitly specifying location—with the idea that different locations will face different environments but similar structures for the production function.[5]

We next review insights from the ecology literature on important 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.

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

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

in economics. 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,"[6] 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.

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

[6] 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.

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).[7]

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.[8]

[7] 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).

[8] 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.

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 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 $n_{i,g}$:

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

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 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, resources are freed up for the remaining species, which can grow their abundances to partially compensate for the population decline from the lost species; this compensatory growth is weaker when species are competing less for the same resources. Species loss will thus 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 $i = 1, \ldots, S_g$.[9] 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 competition for common resources is so intense that each member of a species in a function one-for-one crowds out another species member in that function. This would represent the case of no niche differentiation.

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 biodiversity 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, function g's ecosystem service production E_g becomes:

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

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

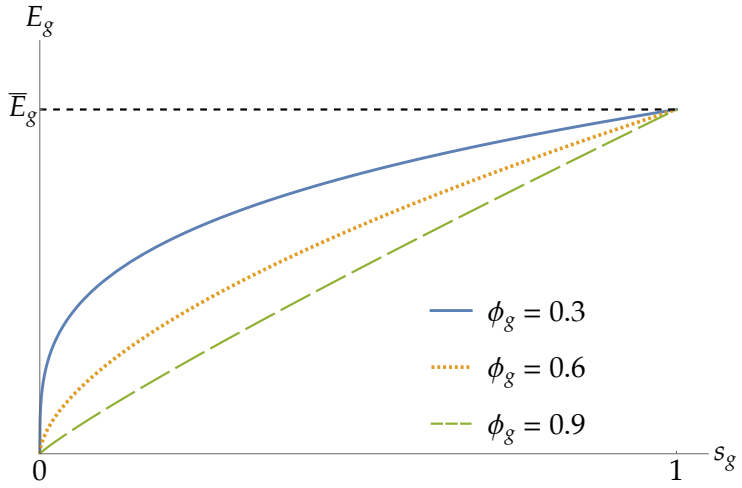
$$\phi_g = \frac{1}{\epsilon_g - 1} + \alpha_g > 0, \tag{6}$$

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 ($s_g = 1$).

[9] 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 B.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 (see also the discussion in Fenichel, Dean and Schmitz, 2024).

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 $\phi_g < 1$.[10] 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.[11] 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.

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:[12]

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

[10] 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.

[11] 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 $\phi_g < 1$.

[12] 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.

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 $\sigma < 1$.[13] Consistent with the empirical ecology literature, this restriction on σ ensures that E goes to zero when any one function is missing entirely.

It is possible to further calibrate σ by comparing the effect of individual and joint increases in the availability of different ecosystem functions on overall ecosystem output. Through the lens of equation (7), the lower the sum of individual marginal effects relative to the joint effect, the lower the elasticity of substitution σ must be. For example, Sutter and Albrecht (2016) studied the joint influence of pest control and pollination on ecosystem functioning, finding "*strong synergistic effects of insect pollination and simulated pest control on yield quantity and quality. Their joint effect increased yield by 23% [...], while their single contributions were 7% and 6%, respectively*." These estimates imply a very low elasticity of substitution between pollination and pest control: calibrating our CES specification to match these reported effects suggests $\sigma \approx 0.1$ (see Appendix B.2 for details on this calculation).

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

2 Biodiversity and Ecosystem Functioning

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

2.1 The Effect of Species Loss on Aggregate Ecosystem Services

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

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

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

[13] 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 $E = \min\{E_1, \ldots, E_G\}$.

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

Proposition 1 further characterizes this marginal effect of species loss on aggregate ecosystem services further, 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 $s_g = S_g/\bar{S}_g \to 0$:*

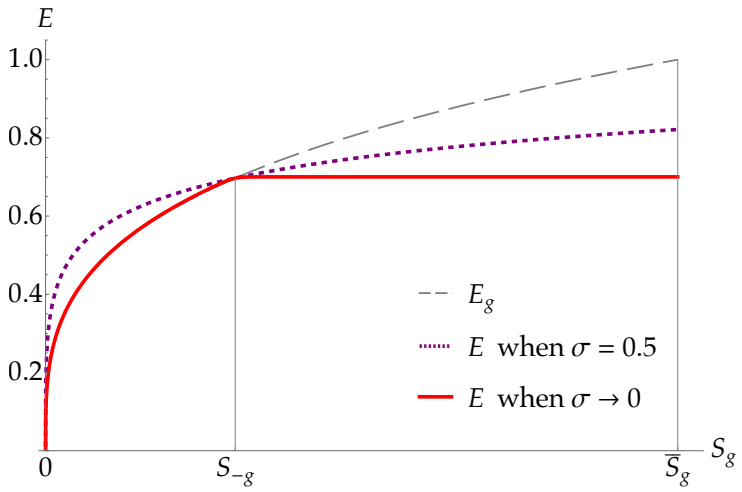
$$\lim_{s_g \to 0} \frac{\partial E}{\partial S_g} = \infty. \tag{10}$$

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 $S_{-g} = 30$.

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

Figure 3: Ecosystem Service Produand 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 $S_g = S_{-g} = \bar{S} = 100$.

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 non-linearities and "tipping points" in the relationship between biodiversity and ecosystem service production, the absence of which from existing models has been lamented by researchers studying the economic effects of biodiversity loss (e.g., Svartzman et al., 2021).

A second implication of the concavity of E with respect to S_g is that the 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. This conclusion is consistent with empirical evidence that past losses of keystone species have had meaningful ecological and economic effects (see Section 3.2). 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):

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

where $\overline{\text{MRS}}_{g,h} = \phi_g/\phi_h \left(\bar{E}_g/\bar{E}_h\right)^{1-1/\sigma}$ is the marginal rate of substitution between functions g and h absent biodiversity loss ($s_g = s_h = 1$). Equation (11) shows how the two sources of concavity in the model, captured by ϕ_g and σ, interact to determine the relative cost of losing species across functions.

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 to 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 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 $\boldsymbol{s} = \{s_g\}_{g=1,\dots,G}$. Throughout this section, we simplify expressions by assuming that $\bar{n}_g$ and $\bar{S}_g$ are the same across functions.

We consider a loss of biodiversity in several functions, given by the vector $d\boldsymbol{s} = \{ds_g\}_g$; 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 $d\boldsymbol{s}$ into three conceptually distinct parts.

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

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

where we denote:

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

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

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

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*

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

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

Finally, the *criticality-abundance gap* $\gamma_g = \mu_g - \omega_g$ captures the difference between function g's marginal contribution to the production of aggregate ecosystem services and its population share. It is positive if 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

[14] 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.

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 $\epsilon_g = \sigma = \infty$).[15]

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, $\text{Cov}\left[\gamma_g, \phi_g / s_g ds_g\right]$, captures how *imbalances in biodiversity* across functions are affected by shocks to biodiversity. This covariance term is equal to zero if species losses occur around a symmetric initial allocation of 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. This term is reminiscent of the literature on the aggregate implications of misallocation of inputs across firms and sectors (e.g., Hsieh and Klenow, 2009; Baqaee and Farhi, 2019*b*). In our setting, differences in the initial allocation of species are often '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 changes in allocative efficiency are only relevant at the second order (Baqaee and Farhi, 2019*a*).[16] 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.

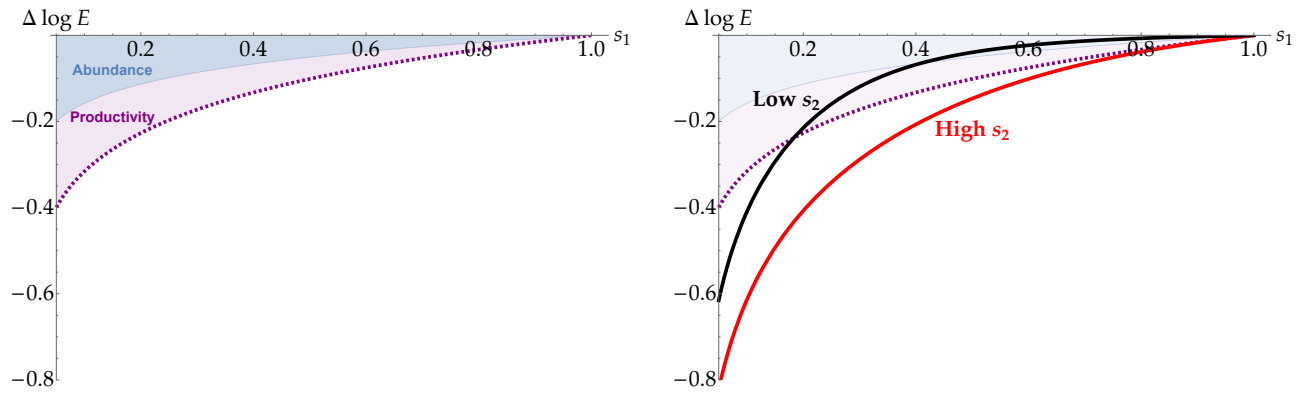
Once again, the intuition for the across-function effects driving the third term is clearest in the limit of no substitution between functions ($\sigma \to 0$). In that case, if species loss occurs in any function except the most critical one, aggregate ecosystem services E remain unchanged in spite 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.

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.

[15] 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.

[16] The reason is that Hulten's theorem applies to efficient economies in which firms are competitive profit-maximizers that face no distortions such as taxes or financial frictions. Here we instead have a highly inefficient production structure because biodiversity losses are not the outcome of a profit-maximization problem.

Figure 4: Decomposing the Effect of Species Loss



Note: Panel A shows the cumulated first two terms in equation (12) for s_1 between 0 and 1. The blue region ("Abundance") corresponds to the first term due to changes in 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., $\epsilon_g \approx 7.7$).

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 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 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*.

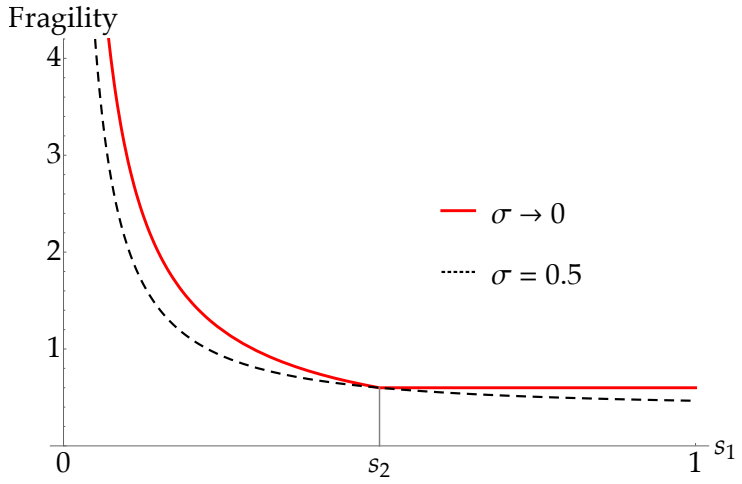
Fragility is also determined by the three forces identified in Proposition 2 and thus depends on the *asymmetry* in past species losses across ecosystem functions. To illustrate the importance of this asymmetry, consider as a minimal example the case of two functions ($G = 2$), with $\phi_1 = \phi_2 = \phi$ 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 $s_1 > 0.5$.

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.

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 B.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.

2.3 Measuring Fragility

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

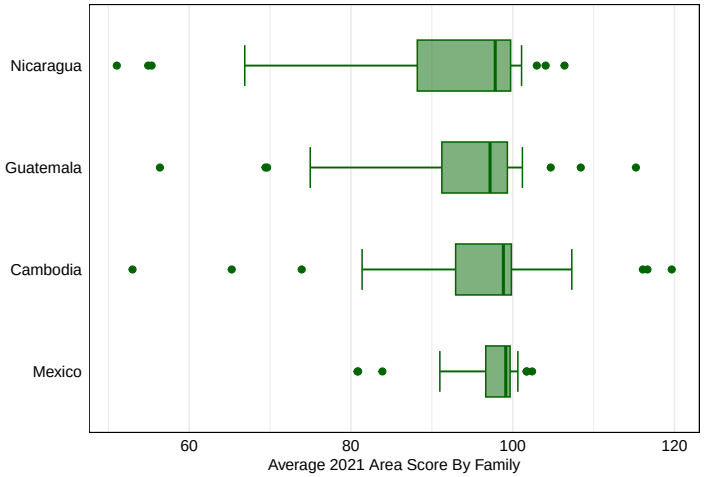
We first derive a first-order approximation to express fragility as a function of two ecosystem properties that can be observed in the data (see Appendix B.9 for details on the approximation): the *average* and *dispersion* of species losses across different functions. To simplify expressions, suppose 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 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.

We then measure the average species loss and its dispersion across functions. To measure the population health of different species, we work with the *Map of Life* database introduced by Jetz, McPherson and Guralnick (2012). This data provides country-level "area scores" calculated annually between 2001

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.

and 2021 for a large number of species of terrestrial vertebrates (see Appendix A 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; Powers and Jetz, 2019). While this data allows us to measure habitat loss for terrestrial vertebrates—which include birds, amphibians, mammals and reptiles—we do not observe species health for marine life, invertebrates, and plants.

To group species by ecosystem function, we obtain taxonomic classifications from the *TetrapodTraits* data of Moura et al. (2024). We observe the order, suborder, and family of each species, which correspond 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 2021, we observe 446 species in the average country, distributed across an average of 82 families, 33 suborders, and 27 orders.

Figure 6 shows the distribution of 2021 family-level average area scores across countries with different levels of average habitat loss. In Mexico and Cambodia, the habitat range for an average species family in 2021 was only 2–4% smaller than in 2001. In Guatemala and Nicaragua, the habitat range for an average family had shrunk by 6–8%. Within countries with similar average habitat loss, the variation in this loss across families can differ widely. At the 10th percentile, family-level habitat ranges declined by 26% in Nicaragua, compared to 18% in Guatemala. One example of a family that has suffered significant habitat loss in Nicaragua is the *Atelidae* family, with a 36% decline in habitat between 2001 and 2021. This family includes species such as the Nicaraguan Spider Monkey, whose endangered status

is largely due to this habitat loss (Cortes-Ortìz et al., 2020). Because these species play a crucial role in seed dispersal, their decline threatens the plant population dynamics necessary to maintain ecosystem health. On the flip side, conservation efforts such as reforesting the Pacific Slope to support species like the Ocelot have successfully expanded the *Felidae* family's habitat range by 0.9% since 2001.[17]

This section has highlighted that existing ecological data allows researchers to measure the various determinants of ecosystem fragility as given in equation (14). In the following section, we will study how these empirical measures of ecosystem fragility are reflected in the price responses of sovereign CDS to aggregate biodiversity news or attention shocks.

3 Biodiversity and the Economy

In this section, we embed the production function for ecosystem services introduced above in an integrated model of the economy and nature. We first add structure to equation (1) and specify an aggregate production function that includes physical capital, land use, and ecosystem services. We then provide empirical evidence from asset prices that suggests biodiversity losses and ecosystem fragility do indeed affect economic activity. In Section 4, we build on this work to study the optimal use of ecological resources that accounts for the feedback between economic activity and biodiversity.

3.1 Ecosystem Services as a Factor of Production

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

$$F(K, E, uL) = \left(\left[K^{\theta} (uL)^{1-\theta} \right]^{\frac{\xi-1}{\xi}} + a_E E^{\frac{\xi-1}{\xi}} \right)^{\frac{\xi}{\xi-1}}. \tag{15}$$

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

Strong vs. weak sustainability. The production function in equation (15) could feature substitutability or complementarity between ecosystem services and other types of capital, depending on the value of ξ. While most of the analysis of the model below holds in both cases, we highlight throughout the implications of the so-called "strong sustainability" hypothesis, corresponding to $\xi < 1$. This concept, proposed by Dietz and Neumayer (2007) and Ekins et al. (2003), emphasizes the difficulties of substituting for several key ecosystem services by increasing other factors of production. This insight was core to

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

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.*"[18]

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

$$\frac{\partial^2 \log F}{\partial \tilde{K} \partial E} = \left(\frac{1}{\xi} - 1\right) \frac{a_E E^{\frac{1}{\xi}} \tilde{K}^{\frac{1}{\xi}}}{(\tilde{K} E^{\frac{1}{\xi}} + a_E E \tilde{K}^{\frac{1}{\xi}})^2}, \tag{16}$$

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

3.2 Biodiversity and the Economy: Case Studies

Our model suggests that certain biodiversity losses can lead to meaningful negative economic effects, in particular if they occur in functions with little functional redundancy. In the next section, we link metrics of biodiversity health—and in particular, measures of ecosystem fragility—to economic activity to provide tests of the key empirical predictions of the model. In this section, we first review several case studies of local extinctions of keystone species and collapses of local ecosystems to provide a clearer understanding of how biodiversity losses can lead to significant economic consequences.

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: a '*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

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

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.

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, darkening skies and suffocating communities. 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.

3.3 Biodiversity and the Economy: Evidence from Asset Prices

While the examples above illustrate the consequences of past ecological disasters, we next present more systematic empirical tests of some of the key implications of the model that relate biodiversity loss to economic activity. Several factors complicate this analysis. First, changes in biodiversity are slow moving and economic output is only observed at low frequencies, which makes identifying a causal relationship between such aggregate quantities challenging. Second, as highlighted by our model, a lack of relationship between biodiversity loss and current economic activity does not by itself imply that there are no meaningful economic effects due to biodiversity loss: instead, even without a large current effect, current species losses make the economy more fragile and thus more exposed to *future* losses.

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

Concretely, we study the effects of news about biodiversity loss on sovereign credit default swap (CDS) spreads, which capture the cost of insurance against default on government debt and thus reflect expectations of aggregate economic tail-risk probabilities. Conceptually, bad news about biodiversity loss will lead to rising CDS spreads if market participants believe that such biodiversity loss will have negative consequences for countries' economic prospects and thus lead to higher default probabilities. Our model predicts that news about biodiversity losses should increase economic risks more for countries with biodiversity that is more degraded on average (Proposition 1); more for countries where the degradation of biodiversity is more uneven across ecosystem functions (Proposition 2); and more for countries where ecosystem services are more binding in the production process (Section 3.1), for example because other factors are more plentiful. This section provides an empirical test of these predictions.

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 CDS, though including non-USD-denominated CDS gives similar results. Our main object of interest is the CDS spread, which is the annual fee to purchase protection against a negative credit event, usually quoted as a fraction of notional amount insured (typically in basis points per year; 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 386,000 weekly changes in CDS spreads for 79 distinct countries between 2001 and 2022 (some countries are only observed in some years). Since the level of CDS spreads varies substantially across countries with different credit risk, we measure changes in CDS spreads in percent relative to the prior week (instead of studying absolute changes). At the 5th percentile of the distribution, CDS spreads fell by 12.1 percent in a week; at the 95th percentile, they increased by 14.9 percent. The 5-year tenor is the most common at 18.9% of the sample, while long maturities of 30 years are the least common at 14.8% of the sample.

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

Biodiversity Destruction. To measure the state of biodiversity in a country, we work with information from the Environmental Performance Index (EPI) published by the Yale Center for Environmental Law & Policy (Wolf et al., 2022). The EPI provides measures of a country's performance on several environmental aspects. We construct our main measure, *BiodiversityDestructionScore*, by aggregating several indicators related to biodiversity and ecosystem vitality (see Appendix A for details): (i) a measure of changes in biological diversity; (ii) a measure of the amount of suitable habitat remaining for each species; and (iii) measures of tree cover loss, grassland loss, wetland loss, and fisheries loss. Since higher values in the EPI indicators represent better environmental outcomes, we reverse the sign so that larger values correspond to greater biodiversity degradation. Since the *BiodiversityDestructionScore* measures biodiversity destruction relative to a baseline in a given country (instead of comparing absolute biodiversity richness across countries), it aligns well with the metric of biodiversity loss used in the model, $s_g = S_g/\bar{S}_g$, which also captures biodiversity loss relative to the initial number of species present.[19]

The EPI is available as of the year 2022, but also includes a baseline version of the indicator "derived from applying the same methodology to data from approximately 10 years prior to current measurements." In our baseline analysis, we average across measures at both points in time to construct our country-level *BiodiversityDestructionScore*. Appendix Table A.1 shows the *BiodiversityDestructionScore* by country, highlighting substantial variation within and across regions. Worldwide, some of the lowest

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

scores (corresponding to the least biodiversity destruction) are observed in the Middle East. The low scores of many Middle Eastern countries reflect the fact that large swaths of their desert landscapes are still relatively un-eroded and endemic species are in comparatively good shape even though they tend to have lower absolute values of species density than other habitats such as rainforests. Countries with the highest scores (corresponding to the most biodiversity destruction) span a wide geographic range with Portugal, Uruguay, Malaysia and Ghana ranking at the top. There is also substantial local variation between countries with similar natural habitats. For instance, Jordan has one of the lowest biodiversity destruction scores while nearby Lebanon has seen substantially more biodiversity destruction.

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

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

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

3.3.2 Empirical Analysis

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

$$\begin{aligned}\Delta CDS_Spread_{i,m,t} = \alpha &+ \beta_1 BiodiversityNews_t \\ &+ \beta_2 BiodiversityNews_t \times BiodiversityDestructionScore_i \\ &+ \beta_3 BiodiversityNews_t \times AcrossFamilyHabitatLossDispersion_i \\ &+ \beta_4 BiodiversityNews_t \times NonNaturalCapitalShare_i \\ &+ \xi_{i,m,year} + \epsilon_{i,m,t}.\end{aligned} \tag{17}$$

$\Delta CDS_Spread_{i,m,t}$ is the percentage change in the CDS spread for country i, at maturity m, in week t. We winsorize $\Delta CDS_Spread_{i,m,t}$ at the 1% level for each country to ensure our results are not driven by outliers. $BiodiversityNews_t$ is the unanticipated component of news about biodiversity loss as described above, with higher values representing more bad news. We standardize $BiodiversityNews_t$ to have mean 0 and standard deviation 1 over the sample weeks. The variables *BiodiversityDestructionScore*, *AcrossFamilyHabitatLossDispersion*, and *NonNaturalCapitalShare* are also standardized to have mean 0 and standard deviation 1 across countries in our sample, which facilitates comparisons of effect sizes across regressors.[20] In our baseline regression, we include country $\times$ year $\times$ maturity fixed effects. We also double cluster standard errors by week and country to account for the fact that all CDS for a given country over time and all CDS in a given week across countries might be affected by common factors.

Results. Table 1 presents estimates of regression (17). In column 1, we only include the biodiversity news index in addition to country $\times$ year $\times$ maturity fixed effects. This specification identifies the average effect of negative biodiversity news across CDS spreads for all countries. Directionally, a one standard deviation increase in adverse biodiversity news is associated with an average increase in CDS spreads of 0.19 percent, but this estimate of the average effect is not statistically significant. The lack of statistical significance and the modest size of the average effect is perhaps not surprising given that, in the time series, many other forces drive CDS spreads, combined with the fact that biodiversity loss might not be a first-order economic concern for many countries.

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

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

Table 1: CDS Spreads and Biodiversity News

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

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

The estimated coefficient on the interaction with across-family dispersion of habitat destruction, β_3, suggests that CDS spreads respond more strongly to negative news in countries where biodiversity loss is more unevenly distributed across ecosystem functions. This supports the notion that habitat destruction that is more concentrated in a few functions increases ecosystem fragility, as in Proposition 2. A one standard deviation increase in habitat destruction dispersion raises the effect of negative biodiversity news on CDS spread changes by 0.047 percentage points. The estimate of the interaction with wealth-share of non-natural capital, β_4, shows that CDS spreads react more strongly to negative biodiversity news in countries with a larger wealth-share of non-natural capital, consistent with the intuition that, in these countries, ecosystem services are more likely to be the constraining factor of production. A one standard deviation higher wealth share of non-natural capital raises the impact of a one standard deviation higher negative biodiversity news on CDS spread changes by 0.077 percentage points.

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

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

It is important to note that these findings need not imply that analysts trading CDS necessarily explicitly consider our three exposure indicators. Instead, the observed relationships more likely result from the fact that in countries with larger past losses of biodiversity, or in countries with more dispersed biodiversity losses across families, 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 more broadly covered in the media in those countries, analysts focusing on these countries would naturally pay more attention to news about biodiversity loss.

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

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

In other words, in countries like Portugal and Malaysia, where biodiversity degradation already disrupts key industries, the economic effects of biodiversity loss are already evidently 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.

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

Biodiversity Risk Exposure. The theoretical model and the empirical work just discussed highlight that a country's exposure to biodiversity risk depends on a range of variables, including the average and asymmetry in species loss, and the extent to which output is constrained by ecosystem services. We next construct a single measure of a country's total physical biodiversity risk exposure that combines these three measures. Specifically, we combine a country's values for the three components of this exposure, *BiodiversityDestructionScore*, *AcrossFamilyHabitatLossDispersion*, and *NonNaturalCapitalShare*, weighting them based on the regression coefficients in column 2 of Table 1. This measure captures how a country's current level of biodiversity influences the impact of negative biodiversity news on CDS spreads. Appendix Table A.10 and Appendix Figure A.5 show the resulting *BiodiversityRiskExposure* for each country with available data. The countries with the biggest exposure are Malaysia, Singapore, and Portugal, while some of the least exposed countries are in the Middle East.

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

4 Optimal Conservation Policies

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

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

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

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

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:

$$\bar{n}_{g,1}(u) = (1 - u)\bar{n}_{g,0}. \tag{18}$$

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

$$s_{g,1}(u) = s_{g,0} - \delta u. \tag{19}$$

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).[21] In turn, as discussed in Section 2, species loss affects ecosystem service production through three distinct forces that are all captured in equation (20). The parameter ϕ determines (i) the net abundance loss above and beyond the one captured by equation (18) 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.

Using equations (7) and (8), future ecosystem services are as follows, where land use u appears twice in equation (20) to reflect the two channels through which it affects ecosystems:

$$E_1 = \left\{ \sum_g \left[\bar{E}_{g,0}(1 - u) \left[s_{g,0} - \delta u \right]^{\phi_g} \right]^{\frac{\sigma - 1}{\sigma}} \right\}^{\frac{\sigma}{\sigma - 1}}. \tag{20}$$

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

Model Solution. We denote by $\eta_{X,t} = \partial \log Y_t / \partial \log X_t$ 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

$$1 - u^* = \Lambda \frac{d \log E_1}{d \log(1 - u)}, \tag{21}$$

where

$$\Lambda = \frac{\beta \eta_{E,1}}{\eta_{L,0} \left(1 + \beta \eta_{K,1}\right)} \tag{22}$$

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 B.5 fully characterizes it. Besides Λ, the key object in the optimality condition in equation (21) is the elasticity of ecosystem services to land conservation (which is also an equilibrium object that depends on u^*). Combining equations (20) and (21), we can express the optimal conservation $1 - u^*$ as:

$$1 - u^* = \Lambda \times \Big\{ \underbrace{1}_{\text{Channel (i)}} + \underbrace{\delta (1 - u^*) \mathcal{F}(\boldsymbol{s}_1)}_{\text{Channel (ii)}} \Big\}, \tag{23}$$

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*

$$1 - u^* = \min \left\{ 1, \frac{\Lambda}{1 - \Lambda \delta \mathcal{F}(\boldsymbol{s}_1)} \right\}, \tag{24}$$

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 (24) 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 (24) is not a closed-form solution because u^* also affects the right-hand side $\mathcal{F}(\boldsymbol{s}_1) = \mathcal{F}(\boldsymbol{s}_0 - \delta u^* \mathbf{1})$, but it is sufficient to derive the main comparative statics in Proposition 3.[22] As shown in Section 2.2, a lower substitutability σ between functions increases fragility and therefore optimal conservation. Optimal conservation decreases with initial biodiversity $\boldsymbol{s}_0$, as an economy starting with more biodiversity has more room to deplete its natural capital before suffering from harmful economic effects. Optimal conservation also increases with the importance of ecosystem services in production a_E and with patience β. Finally, the complementarity between physical and natural capital captured by $\xi < 1$ implies that capital-rich countries, with a higher K_0, should invest more in biodiversity preservation, by reducing their land use. The reason is that capital-rich countries are able to save more out of their current output, and thus reach a higher future physical capital K_1. As a result, in the future (at $t = 1$), natural capital will be the relatively scarcer factor of production in those richer countries, which implies that conservation of natural capital has a higher return and should optimally be higher.

Extension 1: Targeted Land Use. A key challenge specific to biodiversity relative to the extraction of other exhaustible resources is that the complexity of ecosystem systems makes it difficult to fine-tune land use to preserve the most critical ecosystem functions. In Appendix B.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 B.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.

[22] In Appendix B.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).

5 Conclusion

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

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

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 the relationship with the economy, and there remain important avenues for extending our analyses. First, the model could feature a richer specification of the input-output relationships across ecosystem functions, 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, the model could be expanded to better incorporate the geographic nature of ecosystems. For example, we could allow the production of ecosystem services in a location to depend on the level of biodiversity in other locations. In addition, some of the ecosystem services can be traded across locations (e.g., timber and food), and this could be explicitly studied in the model. Fourth, understanding the interactions between climate change and biodiversity loss—especially how carbon sinks, climate change, and species loss feed back into one another—also represents a promising avenue of theoretical and empirical study (see Giglio et al., 2025, for a first step).

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

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A Empirical Analysis - Further Details

In this Appendix, we provide further details on the data source and data construction steps behind the results presented in Sections 2.3 and 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.

A.1 Details on Data Sources and Sample Construction

Map of Life Data. To proxy species abundance in each country over time, we use the Map of Life database compiled by Jetz, McPherson and Guralnick (2012). The Map of Life aggregates 532 species range datasets, including both direct observations and expert predictions, to provide comprehensive spatial data on habitat boundaries, size, and suitability for terrestrial vertebrates. This spatial data is used to calculate area scores at the species-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. We use this habitat score as an alternative measure of habitat destruction for our robustness checks in Table A.11, and find similar results to our baseline estimates using 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 and calculate unweighted average area scores across all species for different definitions of functional groups. We then calculate the unweighted across-group standard deviations (and mean) of habitat loss in each country in 2021. In Table A.2, we report summary statistics by country. For example, for Argentina we have data on 1,119 unique species belonging to 132 families, 48 suborders, and 40 orders. Across these species, the 2021 area scores have a standard deviation of 8.09; the within-family average area scores have a standard deviation of 5.8 across families. In Figures A.2 and A.3, we map the across-family and across-order means and standard deviations of area scores in 2021 for countries in our regression sample. In Table A.3, we report the count, across-group mean, and across-group standard deviation of area scores in 2021 for countries outside our sample.

Our baseline measure for the across-function dispersion of biodiversity losses is the across-family standard deviation of the area score in 2021. 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 (family and suborder), and two time points (2015 and 2021). These correlations presented in Tables A.4 and A.5 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".[23] The "Species Habitat Index" (SHI) is derived from the Map of Life data discussed above, where a country's annual SHI value is the average habitat score of all species occurring in that country in that year, weighted by the proportion of their global range found within that country. This index captures the extent *"of suitable habitat within a country that remains intact for each species in that country."* Since habitat loss is one of the key drivers of extinction, it captures the *"potential population losses ... and ...extinction risks of individual species."* (Wolf et al., 2022, p111). The "Biodiversity Habitat Index" (BHI) is obtained by analyzing remotely-sensed forest change and land-cover change datasets using the PREDICTS model (Newbold et al., 2015) to predict habitat conditions. This index captures the *"change in biological diversity within a country due to habitat loss, degradation, and fragmentation across that country"* (Wolf et al., 2022, p102).

In addition to these two indicators from the "Biodiversity & Habitat" category, our measure also includes the indicators in the "Ecosystem Services" and "Fisheries" category. 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 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

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

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 average over the measures at the two points in time. Table A.8 shows that the EPI-based measure of biodiversity obtained by averaging the baseline and the 2022 values is very similar to the measure based on 2022 data alone. Table A.9 further shows that the correlation between the baseline, the measure as of 2022, and their average, all exceed 83%. In robustness checks, we also show that our results are similar when using only the most recent measures from 2022.

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

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

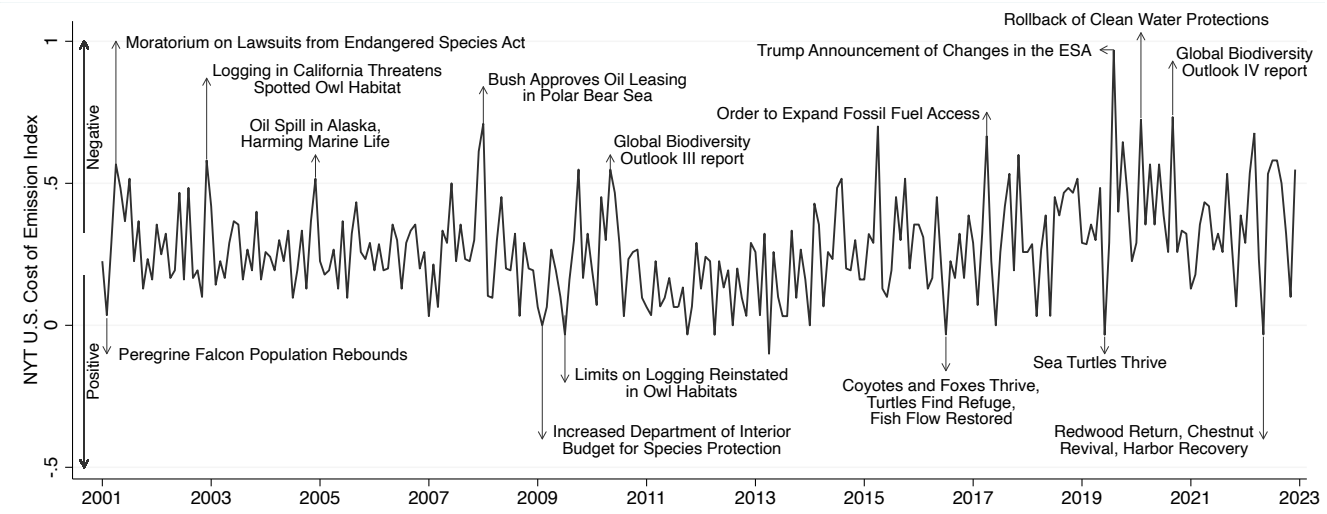
We measure a country's share of non-natural capital by the complement of the share of renewable natural resources of a country's total wealth. We obtain this measure from the Notre Dame Global Adaptation Initiative (2025) project, which collects and makes publicly available a variety of measures of country's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

Correlation Across Measures. Table A.9 shows the correlation between our different country level measures. Our main measure of average biodiversityloss, *Biodiversity Destruction Score-Avg*, is essentially uncorrelated with the *Across-Family Dispersion of Area Scores*. This suggests that the dispersion of habitat loss is a distinct measure from total habitat losses. The *Wealth-Share of Non-Natural Capital* is negatively correlated with both the *Biodiversity Destruction Score-Avg* and the *Across-Family Dispersion of Area Scores*, with a correlation coefficient of minus 13% and minus 22% respectively. This reflects that our 3 measures capture very different concepts. Our EPI-based measure captures how much biodiversity has degraded in a given country relative to its original state. Our Map of Life-based measure captures the dispersion of this biodiversity degradation in a given country relative to its original state. The *Wealth-Share of Non-Natural Capital*, on the other hand, measures absolute values of non-natural capital relative to a country's total wealth. Hence, it will be low if absolute values of renewable natural resources are high, irrespective of the extent or dispersion of degradation. As outlined in Section 3.3, biodiversity is preserved the most in many countries of the Middle East, which are dominated by desert landscapes. Therefore renewable natural capital resources are not necessarily high in absolute values compared to countries with habitats naturally richer in biodiversity but possibly more depleted. In addition, the share of non-natural capital is higher for countries with substantial amounts of other capital irrespective of the state of biodiversity.

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

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

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



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

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

A.2 Robustness Tests

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

stewardship by capping area scores at 100 for species in countries with less than 0.05% stewardship. The results are very similar regardless of the measure of the dispersion of habitat destruction.

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

Table A.13 explores the robustness of our results to using various time periods for the wealth-share of non-natural capital. Column 1 replicates the baseline specification from Table 1, using the average "Wealth-Share of Non-Natural Capital" across all available years (1995, 2000, and 2005) for each country, obtained from the ND-GAIN database (Notre Dame Global Adaptation Initiative, 2025). Columns 2, 3, and 4 use the same measure, restricted to 1995, 2000, and 2005 respectively. The results are similar irrespective of the time period used.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

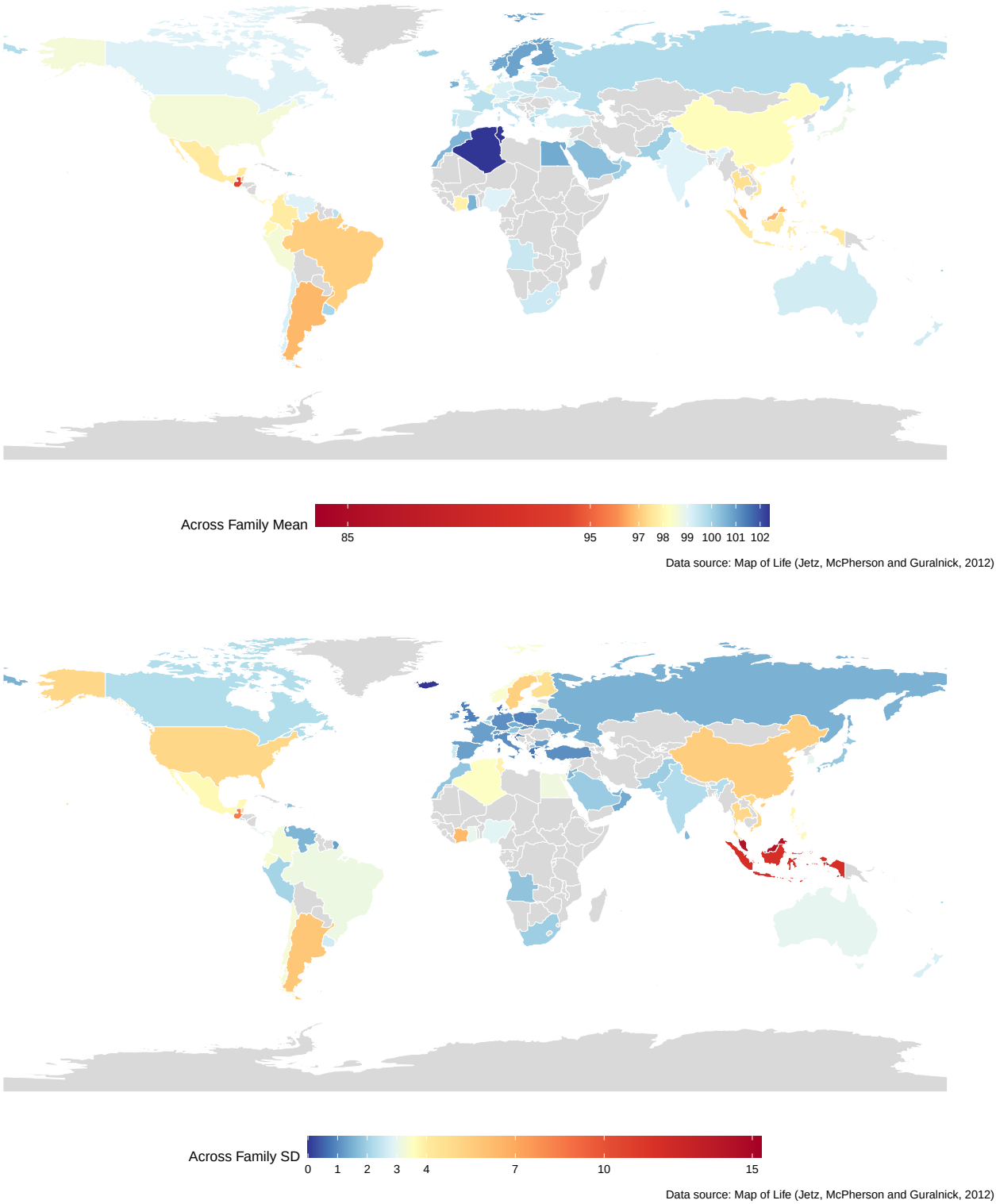
Note: The table shows the group count, as well as the mean and standard deviation of area scores across species, families, suborders and orders in 2021 for each country excluded from the final regression sample.

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

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

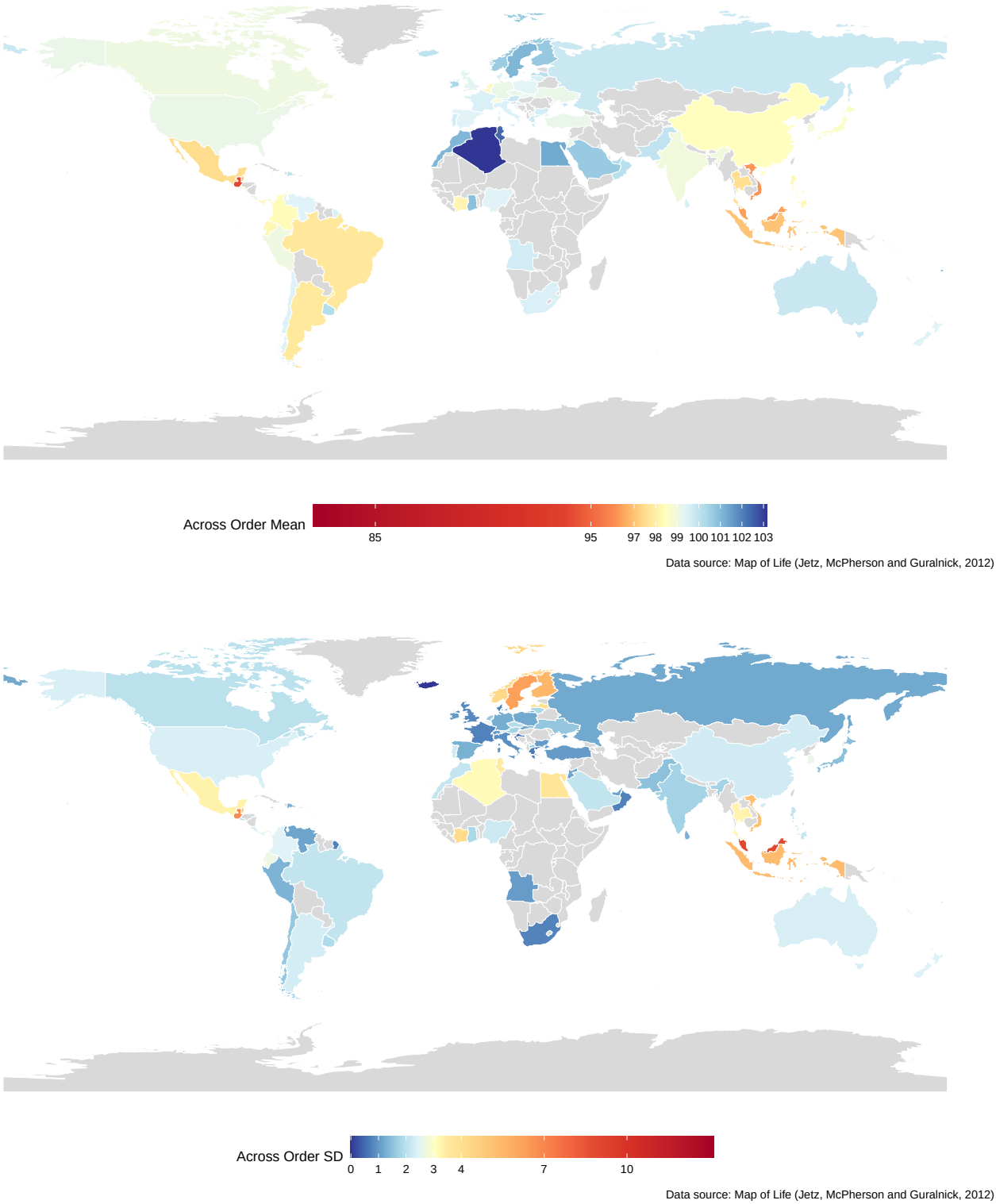
Note: The table presents correlations for all combinations of three score types—SD, p10, and min area (with p10 and min reversed)—across two taxonomic levels (family and suborder) and two years (2015 and 2021). This yields a total of 12 correlation values, between different measures of imbalance in habitat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

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



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

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



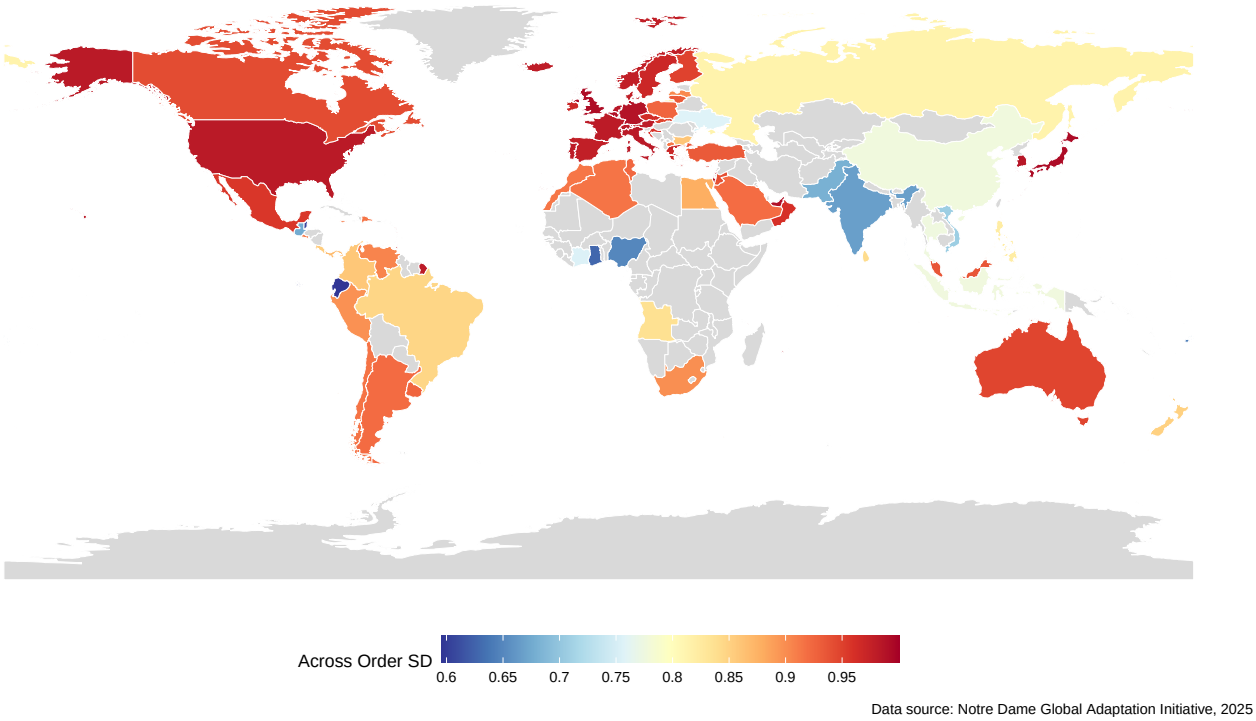
Note: This map shows the across-order mean and standard deviation of area scores in 2021 for each country in our final regression sample.

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

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

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

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



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

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

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

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

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

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

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

Table A.8: Summary Statistics

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

Note: The table presents summary statistics of our regression sample. The top part shows summary statistics of our regression sample of weekly changes in CDS spreads as described in section 3.3 and section A. "CDS spread level (bps)" is the absolute CDS spread in basis points, winsorized at 1% at the top and bottom. "Change in CDS spread level (weekly)" is the change in CDS spread from the prior week, expressed in basis points and winsorized at 1% at the top and bottom. "% Change in CDS spread (weekly)" is the percentage change in the CDS spread from the prior week, winsorized at 1% at the top and bottom. "Biodiversity News (AR(1) Residuals)" are the AR(1) residuals of an index measuring coverage of biodiversity loss in the New York Times, as produced by Giglio, Kelly and Stroebel (2021). "Biodiversity Destruction Score" includes the indicators for the change in biological diversity that has occurred in a country and for the amount of suitable habitat remaining for each species from the EPI's biodiversity and habitat category. In addition, it includes indicators on ecosystem services (loss in tree cover, grassland and wetlands) and fisheries. These indicators are available in 2022 and as a baseline measure around 2012. "Across-Family Dispersion of Habitat Destruction" is the across-family standard deviation of average habitat loss by family. "Wealth-Share of Non-Natural Capital" is the share of a country's wealth that is not derived from renewable natural capital, based on the World Bank's wealth accounting data. We standardize the "Biodiversity News", "Biodiversity Destruction Score", "Wealth-Share of Non-Natural Capital" and "Across-Family Dispersion of Habitat Destruction" to have mean zero and standard deviation of 1 across all countries in our sample. However, in the regression sample, the observation weighted mean and standard deviation differ slightly since the sample is unbalanced across maturities and time.

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

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

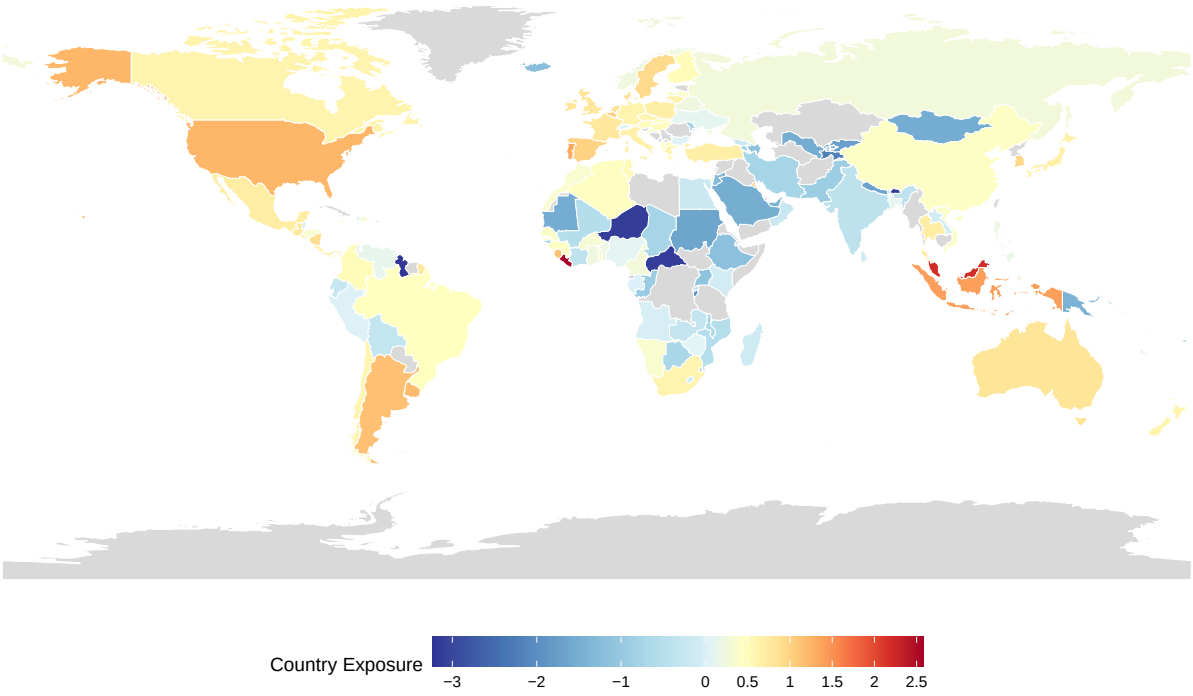
Note: The table shows the correlation between our measures of biodiversity reliance and degradation. "Biodiversity Destruction Score" includes indicators for the change in biological diversity within a country and for the amount of suitable habitat remaining for each species from the biodiversity and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

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

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

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

Figure A.5: Biodiversity Risk Exposure by Country (All Countries)



Note: This map shows the standardized weighted sum of country-level exposure to biodiversity risk, calculated using regression coefficients from column 2 in Table 1 for all countries with data for each of our 3 measures of biodiversity degradation: "Biodiversity Destruction Score", "Across-Family Dispersion of Area Scores", and "Wealth-Share of Non-Natural Capital". Here, each measure is standardized across all countries, not just the in-sample countries.

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

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

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

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

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

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

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

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

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

B Theoretical Appendix — 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.

B.1 Extension to within-function asymmetry of abundance

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

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

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

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

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

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

B.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

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

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

We can then define

$$\text{Single effect 1} = \frac{\mathcal{E}(\bar{E}(1+\Delta_1), \bar{E}, \sigma) - \mathcal{E}(\bar{E}, \bar{E}, \sigma)}{\mathcal{E}(\bar{E}, \bar{E}, \sigma)} = \frac{\mathcal{E}(1+\Delta_1, 1, \sigma) - \mathcal{E}(1,1,\sigma)}{\mathcal{E}(1,1,\sigma)}$$

$$\text{Single effect 2} = \frac{\mathcal{E}(\bar{E}, \bar{E}(1+\Delta_2), \sigma) - \mathcal{E}(\bar{E}, \bar{E}, \sigma)}{\mathcal{E}(\bar{E}, \bar{E}, \sigma)} = \frac{\mathcal{E}(1, 1+\Delta_2, \sigma) - \mathcal{E}(1,1,\sigma)}{\mathcal{E}(1,1,\sigma)}$$

$$\text{Joint effect} = \frac{\mathcal{E}(\bar{E}(1+\Delta_1), \bar{E}(1+\Delta_2), \sigma) - \mathcal{E}(\bar{E}, \bar{E}, \bar{E})}{\mathcal{E}(\bar{E}, \bar{E}, \sigma)} = \frac{\mathcal{E}(1+\Delta_1, 1+\Delta_2, \sigma) - \mathcal{E}(1,1,\sigma)}{\mathcal{E}(1,1,\sigma)}$$

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 $\sigma \approx 0.1$.

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

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.

B.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.[25]

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:

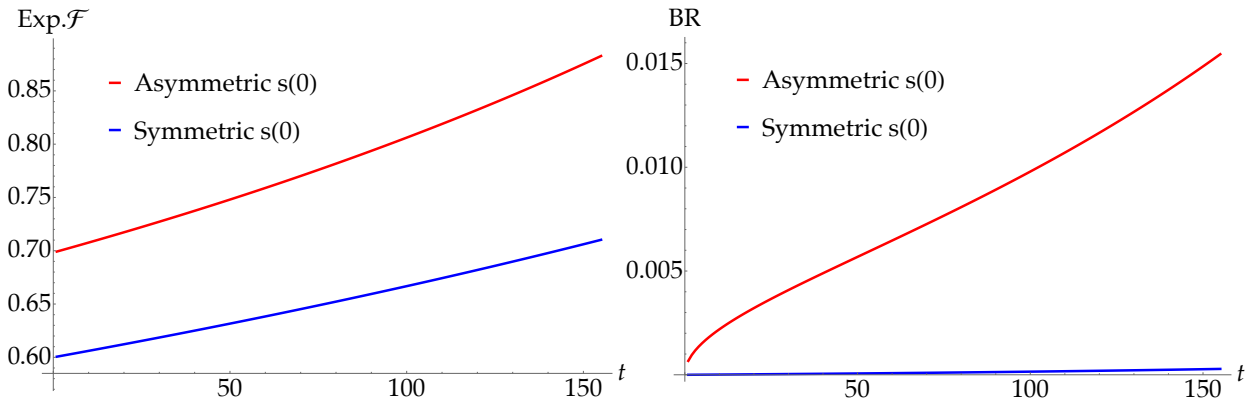
$$\mathrm{BR}(t) = \frac{1}{\delta}\sqrt{\mathbb{E}_0\left[\mathrm{Var}(d\log E(t))\right]} \tag{A.1}$$

$$= \sqrt{\mathbb{E}_0\left[\mathrm{Var}(\mathcal{F}(\boldsymbol{s}(t)))\right]} \tag{A.2}$$

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 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.

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

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

Figure B.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.

B.5 Closed-Form Expression for Λ

With our production function (15) 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 $X_t = K_t^{\theta}(u_t L)^{1-\theta}/E_t$.

B.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 $\sigma > 0$

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

B.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 (24) 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.

B.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

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

B.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

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

Hence

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

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

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

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

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

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

Hence

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

Substituting

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

yields

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

C Theoretical Appendix - 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 $\text{Cov}(x,y) = \sum_g (x_g - \frac{1}{G}\sum_j x_j)(y_g - \frac{1}{G}\sum_j y_j)$. Define for any $\boldsymbol{s} = \{s_g\}_{g=1}^G$ and $\boldsymbol{\theta} = \{\theta_g\}_{g=1}^G$ the function:

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

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

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:

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

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 $\bar{\boldsymbol{n}}$. 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

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

hence the optimal conservation satisfies

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

The optimality condition with respect to K_1 implies

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

therefore

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

where

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

Differentiating

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

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

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

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

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

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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