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THE ECONOMICS OF BIODIVERSITY LOSS

Stefano Giglio
Theresa Kuchler
Johannes Stroebel
Olivier Wang

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ABSTRACT

We explore the economic effects of biodiversity loss by developing an ecologically-founded model that captures how different species interact to deliver the ecosystem services that complement other factors of economic production. Aggregate ecosystem services are produced by combining several non-substitutable ecosystem functions such as pollination and water filtration, which are each provided by many substitutable species playing similar roles. As a result, economic output is an increasing but highly concave function of species richness. The marginal economic value of a species depends on three factors: (i) the number of similar species within its ecosystem function, (ii) the marginal importance of the affected function for overall ecosystem productivity, and (iii) the extent to which ecosystem services constrain economic output in each country. Using our framework, we derive expressions for the fragility of ecosystem service provision and its evolution over time, which depends, among other things, on the distribution of biodiversity losses across ecosystem functions. We discuss how these fragility measures can help policymakers assess the risks induced by biodiversity loss and prioritize conservation efforts. We also embed our model of ecosystem service production in a standard economic model to study optimal land use when land use raises output at the cost of reducing biodiversity. We find that even in settings where species loss does not reduce output substantially today, it lowers growth opportunities and reduces resilience to future species loss, especially when past species loss has been asymmetric across functions. Consistent with these predictions of our model, we show empirically that news about biodiversity loss increases spreads on credit default swaps (CDS) more for countries with more depleted ecosystems.

Stefano Giglio
Yale School of Management
165 Whitney Avenue
New Haven, CT 06520
and NBER
stefano.giglio@yale.edu

Theresa Kuchler
Stern School of Business
New York University
44 West 4th Street
New York, NY 10012
and NBER
tkuchler@stern.nyu.edu

Johannes Stroebel
Stern School of Business
New York University
44 West 4th Street
New York, NY 10012
and NBER
johannes.stroebel@nyu.edu

Olivier Wang
New York University
Kaufman Management Center
44 West Fourth Street
New York, NY 10012
olivier.wang@nyu.edu

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

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

Given this common perception that nature and biodiversity loss might significantly affect economic activity, there is a notable lack of research that would facilitate a fuller understanding and quantification of the interactions between biodiversity and the economy.[1] To the extent that nature's contributions to economic growth are incorporated in economic models at all, this is usually done by considering a monolithic stock of "natural capital" that enters the production function. While such approaches have been helpful to understand some aspects of the economic importance of nature, they are silent about how to aggregate the totality of nature into this singular measure of natural capital. Indeed, by abstracting from the interactions between different species, these models have no role for bio*diversity*, and provide no framework for exploring how various species contribute to economic activity.

In this paper, we aim to fill this gap by developing a model of how biodiversity affects 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 species richness, or the number of species present (Hooper et al., 2005). Our model thus studies how different species interact to produce the aggregate *ecosystem services* that enter more familiar economic production functions (see Daily et al., 1997, 2000; Chichilnisky and Heal, 1998; Heal, 2000; Dasgupta, Kinzig and Perrings, 2013). These ecosystem services include provisioning services such as food, fuel, timber, and raw materials for pharmaceutical R&D, as well as regulating services such as the provision of clean air and water, carbon sequestration, pest regulation, and natural hazard regulation (Millennium Ecosystem Assessment, 2005; Döhring et al., 2023; OECD, 2023). Our production

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[1] This is in contrast to the more advanced work that integrates (simple) 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).

function for aggregate ecosystem services is grounded in insights from the ecology literature but remains sufficiently tractable to be incorporated into more general economic models. It allows us to characterize the determinants of the marginal economic values of different species and the fragility of ecosystem service provision, and thus helps to 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 groups of species interact to contribute to a productive ecosystem (e.g., Diaz and Cabido, 2001; Hooper et al., 2005; Cadotte, Carscadden and Mirotchnick, 2011; Cardinale et al., 2012). At the highest level, we capture the fact that the aggregate output from a healthy ecosystem depends on the often complex interactions of many different *ecosystem functions*, including those referred to as 'regulating' and 'supporting' functions: pollination, nutrient recycling, water purification, pest control, and many more. We model the combination of these functions into an aggregate ecosystem service flow via a constant-elasticity-of-substitution (CES) aggregator familiar to economists (see Arrow et al., 1961; Dixit and Stiglitz, 1977). Consistent with insights from the ecology literature, different functions are complements in the production of aggregate ecosystem services (i.e., they have an elasticity of substitution $\sigma < 1$), capturing the idea that healthy and productive ecosystems are hard to sustain when key functions are missing and that a decline in the availability of one function cannot easily be compensated for by the growth of other functions (Sekercioglu, 2010).[2]

When modeling the provision of each ecosystem function, we capture that there are usually multiple species playing similar functional roles (e.g., many insect species provide pollination services). We assign each species to its primary ecosystem function, and model the total output of a function as another CES aggregator across the number of individuals in each species. Within this function-level aggregator, different species are highly substitutable, but not perfectly so (i.e., the elasticity of substitution is $1 < \epsilon < \infty$). This approach implies that a function with two species of 50 members each has higher output than a function with 100 members of a single species, consistent with the "biodiversity-productivity" relationship documented in the ecology literature, which found function-level output to be an increasing but concave function of species richness. This relationship results from *niche differentiation*, whereby different species in the same function vary on dimensions that ensure they inhibit other species less than members of their own species. For example, when plant species with roots of different lengths are present, more nutrients can be extracted and a larger biomass sustained than in monocultures.

This nested-CES set-up with complementarities across functions and substitutability across species within each function generates highly non-linear and context-dependent effects of biodiversity loss on the provision of aggregate ecosystem services. In a species-rich function, functional redundancy ensures that species loss has little effect on functional productivity, since many other species with similar functional roles will exhibit compensatory growth. As biodiversity loss reduces the number of remaining similar species in a function, the loss of any one of them has increasingly large effects, until the remaining species become "keystone species" whose extinction will lead to large negative effects on ecosystem

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[2] For example, the loss of pollination services—the transfer of pollen between the male and female parts of flowers that enables fertilization and reproduction–would lead to a substantial decline in crop yields. Beyond its immediate effect on the food supply available to most trophic levels, this reduction in plant-based biomass would, in turn, lead to a decline in many other ecosystem services, such as water filtration, carbon sequestration, and the avoidance of soil erosion; and each of these would have further negative effects on the overall ecosystem (Potts et al., 2016; Christmann, 2019).

and economic output. In other words, species loss has two effects, reducing both the *productivity* of an ecosystem function and its *resilience* to further species loss, with larger effects at lower initial levels of species richness. The complementarity across functions in the production of aggregate ecosystem services amplifies this concavity: even after a function's specific ecosystem service production has started to decline, the provision of aggregate ecosystem services is not affected until the affected function's productivity has fallen enough such that it becomes a constraining function within the ecosystem.[3] As such, our model naturally generates substantial non-linearities and tipping points whose absence from existing economic models of nature loss has been previously criticized (see, e.g., Svartzman et al., 2021).

We use our model to characterize the aggregate impact of an arbitrary distribution of species losses across functions, and propose a decomposition reminiscent of the literature on the economic effects of input misallocation across firms (Hsieh and Klenow, 2009; Baqaee and Farhi, 2019*b*). Our model yields a tractable measure of the *fragility of ecosystem services*—that is, the sensitivity of aggregate ecosystem service output to further biodiversity shocks—and how it is affected by species loss over time. Our fragility measure highlights three conceptually distinct ways in which nature loss affects ecosystem services production: (i) a direct reduction in total abundance of ecosystem members (i.e., population or biomass); (ii) a within-function productivity impact of species loss through reductions in niche differentiation, with larger effects in functions that have suffered more prior species loss; and (iii) an effect related to uneven distributions of past species losses across ecosystem functions, which can amplify the impact of species losses in already depleted functions due to the complementarity of these functions in the production of aggregate ecosystem services. We show that, over time, idiosyncratic shocks increase the dispersion of realized species losses across functions, and that this raises both average fragility and *biodiversity risk*, defined as the dispersion of outcomes that can result from a given species loss shock.

With this production function for ecosystem services in hand, we consider the effects of biodiversity loss on economic activity. Following a large literature, we propose an economic production function that uses ecosystem services as complements to other factors of production (land and capital) to capture the idea that it is hard to substitute for the loss of ecosystem services through an increased use of other factors (Dasgupta, 2021). The relationship between economic output and biodiversity loss inherits many of the properties of the relationship between biodiversity loss and the production of aggregate ecosystem services. The complementarity between factors of production further amplifies the concavity of the relationship between biodiversity and output: losses of aggregate ecosystem services in response to biodiversity loss will only affect aggregate economic output in places where those ecosystem services—and not, for example, the availability of physical capital—are the primary constraint on aggregate output.

We then consider the joint feedback between economic activity and biodiversity loss, allowing us to explore the longer-run effects of biodiversity loss on economic growth and the implication for the optimal use of natural resources. Since land-use changes have been the key driver of global biodiversity loss (IPBES, 2019; Jaureguiberry et al., 2022), we study how land use choices affect ecosystems and economic output. When a larger share of land is allocated to generate economic output, the biomass of

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

each species falls, leading to an increase in the probability of species extinction in response to random shocks (Cleland, 2011). While some recovery of ecosystems occurs both in the short term (as remaining species grow to partially compensate for extinctions) and the very long run (where biodiversity can recover through genetic mutation), biodiversity losses reduce the productivity of the ecosystem and increase its fragility, making it more sensitive to further losses from continued land use.

We solve for the optimal land use of a country that recognizes not only the benefits of land use for production, but also the current and future costs due to biodiversity loss. Within a stylized model of this intertemporal choice, we show that due to the fact that the persistence of biodiversity loss and its effect on fragility, a rational agent that cares about the long-term will be particularly conservative in using land today. As countries grow and accumulate physical capital, the complementarity between ecosystem services and other factors makes them more conservative with respect to land use that destroys biodiversity: for a developed country with abundance of physical capital, the "constraining factor" is ecosystem services, and therefore their preservation becomes more important. Conversely, for a developing country with more ecosystem resources than physical capital, it is optimal to use more land (and thus destroy biodiversity). We also show that for a given path of physical capital over time, countries that uses more land today trade off current output for future output, thus reducing growth opportunities. In situations where the discount factor of the decision-makers might not fully internalize the future costs (i.e., the decision might be excessively myopic), this leads to an over-destruction of biodiversity.

In the final part of the paper, we provide empirical evidence that (future) biodiversity loss materially affects countries' economic output. We show that spreads on country-level credit default swap (CDS) —a measure of investors' perceived probability that a country will default on its debt—increase substantially when investors receive negative news about aggregate biodiversity loss, as measured in Giglio et al. (2023). In line with the implications from our model we find that such news leads to particularly large increases in CDS spreads among countries with relatively more depleted ecosystems as captured by several independent indicators of ecosystem health. Similarly, we find larger increases in CDS spreads among countries where ecosystem services are more likely to be the constraining factor for aggregate output. These finding are consistent with investors realizing that biodiversity loss might have large effects on the resilience of the local economies to further species loss, particularly when biodiversity is already more depleted or ecosystem services are more binding for production.

Policy Implications. Our modeling framework has a number of 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: the argument that the lack of compelling narratives of how the large *past* losses of biodiversity have not led to significant declines in economic output means that *future* biodiversity loss will also have no large economic effects. The non-linear relationship between species richness and economic output that follows naturally from the ecology literature highlights that the correct conclusion is quite different, and that a key effect of past losses of biodiversity has been to create a situation where any *future* losses of biodiversity will have increasingly large economic effects. More generally, our work highlights the state- and context-dependence of the economic effects of biodiversity loss and shows that any generalization from existing empirical studies of biodiversity loss needs to condition on measures of the ex-ante fragility of ecosystem service production.

Our modeling approach also emphasizes that different species are differentially important for overall ecosystem service production, and thus economic activity. Indeed, 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, which can be useful to policy makers across a range of settings. First, it can inform the optimal design of Pigouvian taxes on economic activities that might lead to local extinctions of various species. Second, it provides a tool to think about the prioritization of conservation efforts in a world where society's willingness to bear costs to protect nature is finite. Third, our framework can be helpful to determine appropriate 'exchange rates' across activities affecting different species in the design of biodiversity offsets in which firms aim to compensate for specific negative biodiversity effects of their activities through conservation efforts that protect other dimensions of biodiversity (McKenney and Kiesecker, 2010).

Our framework can also help policy makers quantify the risks from ecosystem services loss for the financial sector (van Toor et al., 2020; Svartzman et al., 2021). A first step taken by regulators hoping to produce such quantifications has been to explore the dependence of economic activity on ecosystem services, arriving at conclusions such as *"75% of all corporate loan exposures in the euro area have a strong dependency on at least one ecosystem service"* (Boldrini et al., 2023). One challenge with interpreting such measures is that they are silent about the actual risk to those firms, which also depend on whether the provision of a particular ecosystem service is at risk from reasonable changes in biodiversity, leading the NGFS (2023) to comment that any findings based on these existing approaches should be *"considered an upper bound estimate of the potential scale of the risk, not the premises of a plausible future."*[4] Our model provides regulators with a framework to focus attention on exposures to those non-resilient ecosystem functions for which plausible losses in biodiversity might actually lead to large productivity declines. Similarly, our expressions for the fragility of ecosystem services will help focus attention on dependencies on ecosystem services provided by less healthy ecosystems, such as those that have seen substantial asymmetric biodiversity loss across different functions.

Our model also highlights how the complementarity of ecosystem services and other factors of production dampens the effects of biodiversity loss on economic output in developing countries where access to physical capital is the key force constraining economic activity. However, this does not mean that there are no economic costs from biodiversity loss in those countries. Indeed, the dynamics between economic output and biodiversity show that even when biodiversity loss does not have large effects on economic output or even resilience today, species loss still imposes the substantial economic cost of reducing the long-run growth potential of countries, whereby, over time, they will need to dedicate larger shares of available land to nature to produce a given amount of ecosystem services at lower levels of biodiversity. These findings thus highlight that the destruction of biodiversity has negative effects on future generations even if it leaves the (economic) welfare of current generations largely unchanged. In settings where current decisions makers have a higher discount rate than a social planner, this would

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[4] To see this, one can take the argument to its pathological extreme: all of economic activity depends on nature, since humans need air to breathe. While true, such arguments are not particularly useful for quantifying the risks of biodiversity loss on output, since reasonable scenarios of nature loss generally do not include the complete disappearance of breathable air.

justify the application of broad-based Pigouvian taxes on the destruction of biodiversity.

Caveats. In an attempt to make progress on one key dimension—how biodiversity loss might affect economic output—we abstract from many important dimensions of the interactions between humans and nature. We hope that future work by us and other researchers can expand on our findings to provide an even more comprehensive overview of the relationships between economic activity and nature.

For example, by exploring the effects of species loss we focus on only one aspect of biodiversity loss, albeit an important one, and a consideration of other dimensions of biodiversity loss could further enrich our framework. We also do not discuss how biodiversity loss might affect the provision of 'cultural ecosystem services' such as recreational opportunities that nature provides, which can enter households' utility functions directly without affecting output. Incorporating such considerations might change the relative importance of different species to mankind, for example if a 'cute' species that create direct utility to humans is not in positions in its ecosystem that assign it a high economic value (Di Minin et al., 2013). We also do not consider the broader ethical question of whether the value of nature is best approached from the anthropogenic perspective of the loss of ecosystem services that are useful to humans, or whether species existence should be given some weight per se.

We intentionally focus this paper on the economic effects of biodiversity loss, which we view as a conceptually distinct challenge to climate change. However, the two clearly interact in important ways that could be explored more explicitly in future work. For example, a key ecosystem service is nature's provision of carbon sinks to mitigate climate change, while a changing climate increases the frequency of extinction shocks to species that are suboptimally adapted to the new climate (Bellard et al., 2012), creating feedback loops between climate change and biodiversity loss that could be explored further.

We also do not explore the economic costs from transition risks such as regulatory restrictions on certain economic activities that degrade nature. Many of the cross-sectional implications of biodiversity loss across industries will come from such regulatory interventions, in particular in the short run (see Giglio et al., 2023). A complete accounting of the financial stability implications of biodiversity loss more broadly thus needs to also consider the effects of plausible regulatory interventions.

Even with these restrictions on the scope of analysis, our modeling approach requires substantial abstractions from the complexities of real world ecosystems and economies. Some of these are obviously necessary to keep the model sufficiently tractable to be useful to economist hoping to understand the interactions between biodiversity and the economy. Nevertheless, our model could be further enriched in several dimensions. For example, a more complete specification of the input-output relationships across ecosystem functions would allow researchers to capture any asymmetries across functions in terms of their importance to overall ecosystem functioning. Similarly, instead of including only an aggregate ecosystem service flow in the economic production function, one could separately model the flow of several ecosystem services that might differ in their substitutability with other factors of production. In the same direction, instead of modeling a homogeneous firm, the model could be extended to consider different industries with varying exposures to different ecosystem services, though this approach would also require specifying the input-output structure across industries to deliver aggregate predictions. While the optimal tradeoff between the added complexity from such extensions and their incremental insights depends on what the resulting model is used for, our hope is that the approach proposed in this paper can be a useful starting point for a further development of our economic toolkits.

Finally, while we make progress in identifying some of the key factors that link biodiversity loss and economic activity, this is just the beginning of the journey towards a comprehensive understanding and effective management of the economic risks from biodiversity loss. For example, it will be challenging to parameterize our expressions for the relative economic value of different species or the fragility of ecosystem services, and doing so will require collaborations between economists and ecologists to analyze biodiversity across different functions within specific ecosystems (see Oliver et al., 2015, for an example of such an assessment of the health of different functions within an ecosystem). Our empirical findings that existing country-level measures of ecosystems health capture important aspects of the exposures of country-level CDS spreads to negative biodiversity news suggests that current ecological methodologies are able to deliver meaningful proxies for ecosystem fragility, and we hope that our modeling approach can help refine the questions to ask ecologists such that their answers are most useful to economists. A key focus of such collaborations between economists and ecologist should also be to better understand the extent to which the complexities of ecosystems provide an inherent limit to the degree of certainty we can have, for example, about the functional redundancy that remains in a given ecosystem (our current modeling approach is silent on such uncertainties). While an appreciation of these uncertainties is crucial from a risk-management perspective, they should not be used as a pretext for inaction: even if we cannot always be certain to be precisely right, acting based on the best information from ecology will likely produce better results than not acting at all, or than treating all species and ecosystems as identically important for economic activity.

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. Since the provision of ecosystems varies across geographies, our modeling approach starts by considering a homogeneous firm in each location ℓ with production function:

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

E^{ℓ} denotes ecosystem services provided in location ℓ and $\mathbf{X}^{\ell}$ denotes other factors of production such as physical capital. For simplicity, we focus on a single final economic good Y^{ℓ} that is produced using a single flow of aggregate ecosystem services E^{ℓ}.[5] In this section, we propose an approach to aggregate the contributions of various species in a location to the production of, E^{ℓ}; in subsequent sections, we explore how changes in biodiversity affect economic output, and how economic activity, in turn, affects biodiversity loss and the level of ecosystem service production. For readability reasons, we drop the location index ℓ in the description of the ecosystem production function that follows.[6] We begin by reviewing key insights from the ecology literature, before discussing how we reflect these insights in

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[5] The model could be generalized to incorporate multiple industries/goods with heterogeneous exposures to different ecosystem services. This 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).

[6] One could extend the model to allow the production of ecosystem services in a locations to depend on the level of biodiversity in other locations. It is also possible to extend the model to allow for trade in some of the ecosysterm services (e.g., timber and food), while keeping other ecosystem services such as soil fertilization non-tradable (or tradable at very high costs only).

our modeling of the *production function of ecosystem services*.

1.1 Ecosystem Service Production: Insights from the Ecology Literature.

An ecosystem is commonly defined as the collection of the living things in a particular area—'biotic' factors such as plants, animals, and organisms—and their interactions with each other and non-living parts of nature—'abiotic' factors such as water and soil. The many complex interactions between such biotic and abiotic factors within an ecosystem produce the ecosystem services that enter the economic production function (e.g., food, timber, some types of energy, etc.).

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 hoping to understand 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).[7] 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 Functions. Functioning ecosystems are based on complex interactions between species across multiple functional groups.[8] Following Hannon (1973), researchers have described this interaction of functional groups using various "ecosystem networks" to capture interdependencies across different species or functions, similar to input-output networks in economics. While the full set of interactions in an ecosystem are *"complex to the point of being impossible to understand"* (Montoya, Pimm and Solé, 2006), a common theme in the ecology literature is that healthy ecosystems are hard to sustain when any one function is missing (Szyrmer and Ulanowicz, 1987; Rapport, 1989; Rapport, Costanza and McMichael, 1998; Williams et al., 2002; Felipe-Lucia, Comín and Bennett, 2014).

While empirical work in ecology shows that ecosystem functioning is usually not limited by a single function, and that output growth in multiple functions can affect ecosystem productivity—something referred to as the "multiple limitation hypothesis"—a common finding is that in any given ecosystem, growth in less abundant resources or functions has the largest effects on overall productivity (Sperfeld, Martin-Creuzburg and Wacker, 2012; Garibaldi et al., 2018; Fijen et al., 2020). This evidence is also consistent with findings of positive interaction effects between different ecosystem functions (Lundin et al., 2013; Soliveres et al., 2016; Lundin et al., 2013; Garibaldi et al., 2018; Chen et al., 2022; Martínez-Salinas et al., 2022). 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,"* highlighting *"the importance of non-additive interactions among*

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[7] Species diversity and functional diversity are closely linked empirically (Bihn, Gebauer and Brandl, 2010; Heino, 2008). At one extreme, monocultures, by definition, can be a member of only one functional group, while settings with more unique species also generally have more functional traits and groups represented (Cadotte, Carscadden and Mirotchnick, 2011).

[8] Some groups of species have mutualistic relationships, whereby members of each functional group benefit from the presence of the others. For example, plants and pollinators each rely in each other for their existence: the pollinator benefits by feeding on the nectar and pollen provided by the flower, while the plant benefits from the ability to reproduce as the pollinator transfers pollen as it moves between flowers (Kearns, Inouye and Waser, 1998). Other bilateral relationships are more antagonistic, for example those between predator and prey or those between herbivores and plants.

ecosystem services." This is consistent with observations by the OECD (2023) that *"the loss or decline in any single ecosystem service, stemming from the degradation or reduction in the stock of biodiversity, is likely to reduce the productivity of other ecosystem services."*

Species Substitutability within Functions. A key ecological observation regarding the effects of biodiversity within functional groups is that (i) more diverse functions are more productive, and that (ii) the productivity gains from further increases in the number of species are lower at higher levels of biodiversity. Discussing the evidence for such a "biodiversity-productivity relationship," Tilman, Isbell and Cowles (2014) concluded 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, in various studies that experimentally controlled the level of plant diversity across plots of land, Naeem et al. (1995), Tilman, Wedin and Knops (1996), Tilman et al. (1997), and Hector et al. (1999) found that total plant productivity was an increasing function of plant diversity, though with smaller marginal effects at higher levels of diversity. Similarly, based on a large-scale observational study, Liang et al. (2016) conclude that *"using ground-sourced data from 777,126 permanent plots, spanning 44 countries and most terrestrial biomes, we reveal a globally consistent positive concave-down biodiversity-productivity relationship."*

A prominent theory explaining the positive relationship between species richness and function-level productivity is that of "niche differentiation." Hooper et al. (2005) explain the underlying mechanism as follows: "*If species use different resources, or the same resources but at different times or different points in space, more of the total available resources are expected to be used by the community. If those resources limit growth, then increasing functional richness should lead to greater total productivity."* Such niche differentiation means that *"each species inhibits itself more than it inhibits the other species,"* allowing for a larger community abundance—that is, more individuals or more biomass—in more diverse functions (Tilman, Isbell and Cowles, 2014). For example, when an ecosystem contains plants with different root lengths, more of the available nutrients can be extracted than when there are fewer species with roots of similar lengths that compete more intensely for the same resources (Loreau, 1998). Similarly, diverse forests with species with tree crowns at varying heights can use the available light more effectively than forests with fewer distinct tree species, leading to increased total stem biomass (Williams et al., 2017). Niche differentiation can also increase the productivity of more diverse functions keeping the total community abundance fixed.[9] For example, when different pollinator species are active at different times of the day, or when pollinators differ in their ability to access certain flowers, overall crop yield can rise with species diversity for given number of individual pollinators (Hoehn et al., 2008; Blüthgen and Klein, 2011).[10]

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[9] The distinction between the effect of biodiversity on community abundance and productivity conditional on community abundance is less clear for some functions, such as carbon sequestration, where productivity is directly related to biomass.

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

A second key finding in the ecology literature is that the output of ecosystem functions varies less in response to environmental fluctuations and species loss at higher levels of biodiversity. The ecological mechanism for such a "biodiversity-stability relationship" is functional redundancy—having multiple species within a group performing a similar function—combined with compensatory growth, the *"widely observed process in which one species within a functional group increases in response to the reduction or loss of another in the same functional group"* (Naeem and Li, 1997). Hooper et al. (2005) describe the mechanism as follows: *"If an ecosystem is subject to a variety of natural and human caused environmental stresses or disturbances, then having a diversity of species [. . .] ought to reduce the likelihood of loss of all species capable of performing particular ecological processes. [. . .] As some species do worse, others do better because of different environmental tolerances or competitive release. [...] In this sense, redundancy of functional effect traits [. . .] act as insurance in carrying out ecological processes."* Evidence for this biodiversity-stability relationship has been found in many settings (e.g., Naeem and Li, 1997; McGrady-Steed, Harris and Morin, 1997). For example, based on a review of 27 biodiversity experiments, Gross et al. (2014) concluded that *"in grasslands, increasing species richness stabilizes whole-community biomass."* Consistent with this experimental evidence, Bai et al. (2004)'s 24-year observational study of Mongolian grasslands found that compensatory growth responses between species in the same functional group stabilized community biomass.

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 a broad group or "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.[11] Our definition of a function is intentionally broad and ensures that their outputs are complements rather than substitutes in the production of aggregate ecosystem services, while different species within a given group are (imperfect) substitutes in fulfilling the function.[12] Within each function, there are S_g unique species, indexed by $i = 1, \ldots, S_g$, with a population $n_{i,g}$ of individuals in each species. We start with the description of ecosystem service production within each function, E_G before turning to the aggregation of the different functional groups to produce aggregate ecosystem services, E.

1.2.1 Substitutability of Species Within a Function

We assume that natural capital in each function g, defined as the stock of populations or *abundances* $\{n_{i,g}\}_{i=1,\ldots,S_g}$, produces a flow of ecosystem services E_g through a constant elasticity of substitution

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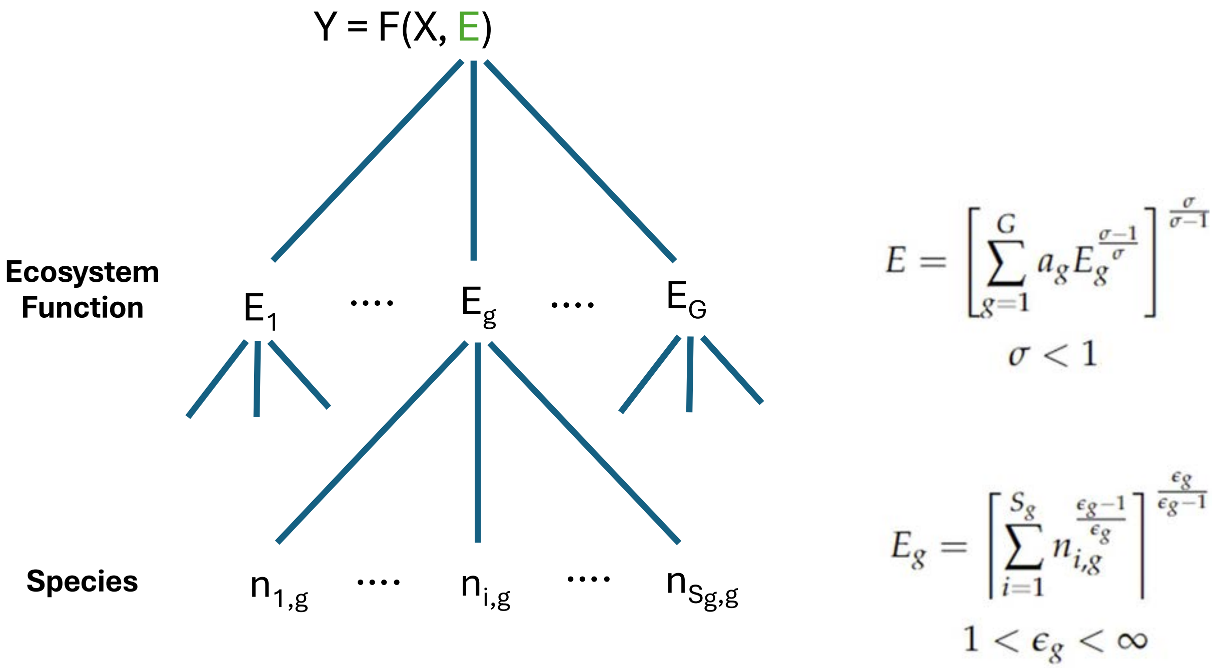
[11] To an economist, this assignment of species to functions is reminiscent of the definition of "sectors" or "industries" as encompassing firms that produce highly substitutable goods and services.

[12] The challenge of delineating functional groups is well appreciated in the ecology literature, and different definitions of functional groups can be helpful for different purpose (Petchey et al., 2009). While cutting the "function space" too narrow will lead to a mechanical convergence of functional and species diversity, the other extreme of grouping different functional groups together may miss large declines in ecosystem productivity from the loss of species with little actual functional redundancy (see the discussions in Naeem and Wright, 2003; Cadotte, Carscadden and Mirotchnick, 2011).

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.

(CES) aggregator across the different species' populations, with elasticity of substitution ϵ_g:

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

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

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

If species become perfect substitutes, $\epsilon_g \to \infty$, then equation (2) is just given by the sum of populations across species $E_g = \sum_{i=1}^{S_g} n_{i,g}$. A finite elasticity captures that, due to niche differentiation, species are not perfect substitutes in terms of ecosystem services production.[13]

Denote as $\bar{S}_g > 1$ the initial, maximal, number of species in functional group g, and let $s_g = S_g/\bar{S}_g$. We focus on biodiversity loss, that is what happens when $S_g \leq \bar{S}_g$. When S_g falls, surviving species in group g adapt partially by growing in response to the decreased competition for common resources, con-

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[13] Our ecologically founded mechanism for the ecological and economic benefits of biodiversity today is quite 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. Here we focus on the immediate benefits of biodiversity in terms of facilitating more productive (and less fragile) ecosystems.

sistent with the ecological evidence for compensatory growth. In principle this could be modeled using Lotka-Volterra models, which describe a full dynamic system governing the evolution of abundances in response to species loss (see Hofbauer and Sigmund, 1998). Instead of solving for the full dynamic path (which is challenging mathematically), we focus on the rest point of the system and assume adaptation depends on a simple parameter $\alpha_g \in [0,1]$. We also impose symmetry among the remaining species in a function, that is, $n_{i,g} = n_g$ for each $i = 1, \ldots, S_g$. We assume that each species' abundance is given by:

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

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

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

is equal to a share $s_g^{\alpha_g} \in [0,1]$ of its maximal level, $\bar{N}_g = \bar{S}_g \bar{n}_g$. The parameter $\alpha_g \in [0,1]$ captures the adaptation of remaining species and can depend on the horizon. The polar case $\alpha_g = 1$ means that $n_g = \bar{n}_g$ and thus captures the short run: following the loss of some species, the remaining species are still at their previous level. The other polar case $\alpha_g = 0$ means that $S_g n_g = \bar{S}_g \bar{n}_g$ and the surviving species expand to fully offset the initial species loss in terms of community abundance within a function. In practice, values of α_g between 0 and 1 are most consistent with the evidence for niche differentiation discussed above. Plugging n_g into the within-function aggregator given by equation (2), ecosystem services produced by function g equal:

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

The first term in equation (4) is the gain from having more biodiversity holding each species' population constant, where we define the following measure of *within-function returns to biodiversity*:

$$v_g = \frac{1}{\epsilon_g - 1},$$

which captures the strength of the "love-of-variety" effect that plays a central role in models of firm dynamics, endogenous growth, and international trade (Matsuyama and Ushchev, 2023; Baqaee et al., 2023). v_g is higher when the substitutability, ϵ_g, is lower, which can be interpreted as species being more differentiated, and v_g vanishes if species become perfect substitutes ($\epsilon_g \to \infty$).

The second term in equation (4) captures the effect of biodiversity on productivity through increasing community abundance N_g. The concavity with $\alpha_g \in (0,1)$ captures the crowding out due to a more intense competition for common resources between species belonging to the same function.

The variables v_g and α_g in equation (4) thus allow for a separate parametrization of the two forces through which niche differentiation can increase E_g: the ability to sustain a more abundant community due to spatial or temporal variation in resource use, and an increase in productivity for a fixed community abundance due to temporal and other variation in performing the ecosystem service. Ultimately function g's ecosystem service production E_g becomes:

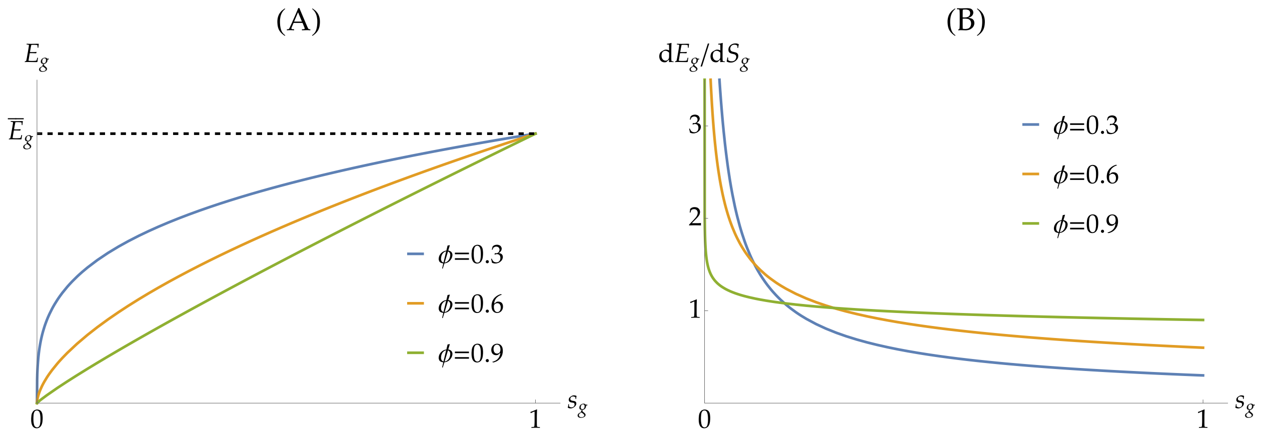
$$E_g = \bar{E}_g s_g^{\phi_g}, \tag{5}$$

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

$$\phi_g = v_g + \alpha_g, \tag{6}$$

and $\bar{E}_g = \bar{n}_g \bar{S}_g^{\frac{\epsilon_g}{\epsilon_g - 1}}$ is the maximum level of ecosystem services attained absent species loss ($s_g = 1$). The parameter ϕ_g is lower if species are more substitutable (higher ϵ_g) and if α_g is lower, which means there is more crowding out in the species' shared environment. We follow the findings from the ecology literature and impose that $\phi_g < 1$, consistent with the empirical observation of a *"positive concave-down biodiversity-productivity relationship"* in the ecology literature (Liang et al., 2016).

Figure 2: Ecosystem Service Production and Biodiversity, Within Group



Note: Panel A shows E_g as a function of s_g for different values of ϕ_g. Panel B shows the equivalent relationships for dE/ds_g.

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

Panel B of Figure 2 shows the *marginal* effect of species loss $ds_g < 0$ on ecosystem services E_g. The concavity of E_g means that the marginal effect is larger when s_g is lower. In other words, our modeling approach naturally incorporates (and microfounds) the presence of "tipping points," the absence of which from existing models has been lamented by researchers hoping to better understand the economic effects of biodiversity loss (e.g., Svartzman et al., 2021).

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. In particular, even though they are often treated as separate observations, a concave biodiversity-productivity relationship immediately delivers the biodiversity-stability relationship: when a function is at the species-rich flat part where additional diversity only has a small effect on productivity, the loss of a particular species has an equivalently small effect on productivity and overall fucntional output varies little in response to external shocks.

Extension to within-function asymmetry of abundance. While our expession 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.[14] 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:

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

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.

1.2.2 Complementarity across Functions

Overall ecosystem services are modeled as aggregating the different ecosystem functions E_g through another CES aggregator, with a_g capturing across-function differences in their importance for the productivity of their ecosystems:[15]

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

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[14] 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.

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

While substitutability is high *within* functions, we assume that functions are complements, that is, that the elasticity of substitution across functions satisfies:[16]

$$\sigma < 1.$$

Consistent with the empirical ecology literature, this restriction on σ ensures that E goes to zero when any one function is missing, and that the productivity of functions $E_j, j \neq i$ is increasing in E_i.

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), we obtain the following expression for the production of aggregate ecosystem services:

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

For each function g, denote

$$E_{-g} = \left(\sum_{j \neq g} a_j E_j^{\frac{\sigma-1}{\sigma}}\right)^{\frac{\sigma}{\sigma-1}} \tag{9}$$

so that

$$E = \left[a_g E_g^{\frac{\sigma-1}{\sigma}} + E_{-g}^{\frac{\sigma-1}{\sigma}}\right]^{\frac{\sigma}{\sigma-1}}. \tag{10}$$

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. Our first result, Proposition 1, describes the marginal impact of species loss on aggregate ecosystem services:

Proposition 1. *E is increasing in S_g, with marginal effects given by:*

$$\frac{\partial E}{\partial S_g} = a_g \phi_g \frac{E}{S_g} \left(\frac{E_g}{E}\right)^{\frac{\sigma-1}{\sigma}}. \tag{11}$$

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[16] 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 $E = min\{a_1 E_1, a_2 E_2, ...\}$. While the evidence from ecology suggests a positive (but still low) elasticity of substitution more consistent with a "multiple limitation hypothesis", this highlights the long intellectual history of the idea that different functions have low elasticities of substitution.

The marginal effect of species loss on ecosystem service production is (i) decreasing in S_g, i.e., E is concave in S_g, and (ii) decreasing in E_g/E, i.e., species loss in functions that are relatively scarce has a stronger effect on E.

Abundant Functions. *Species loss around $\bar{S}_g$ does not affect the aggregate provision of ecosystem services if:*

(i) Function g is abundantly provided, i.e., $\bar{E}_g \to \infty$, or

(ii) Holding $\bar{E}_g$ fixed, the number of species providing function g is large, i.e., $\bar{S}_g \to \infty$.

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

$$\lim_{S_g/\bar{S}_g \to 0} \frac{\partial E}{\partial S_g} = \infty. \tag{12}$$

Discussion. One implication of the concavity of E with respect to S_g is that we cannot extrapolate any observed small effects of initial species loss to understand what will happen as S_g continues to decline. While this was already apparent from the concavity of function-level output E_g (see Section 1.2.1), Panel A of Figure 3 highlights that the complementarity across functions, captured by $\sigma < 1$, further amplifies the concavity at the function level due to $\phi_g < 1$. In this example, the maximal number of species per function is $\bar{S} = 100$, but functions $j \neq g$ have already suffered species loss, bringing S_{-g} down to 10. The Figure shows that even after species loss in function g has started to negatively affect the provision of E_g, this will only affect overall ecosystem productivity E once function g becomes sufficiently limiting for the ecosystem as a whole. This intuition is most transparent when considering the case of extreme complementarity ($\sigma \to 0$), which corresponds to a Leontief aggregator $E = \min\{a_1E_1, ..., a_GE_G\}$, shown as a red line in Panel A of Figure 3. 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 ecosystem service production in function g have no impact on E until g becomes the limiting function, which happens once S_g falls below $S_{-g} = 10$. Similarly, Panel B of Figure 3 shows that, for a given value of σ, function g can sustain a larger loss of species before overall ecosystem productivity falls in ecosystems where other functions E_{-g} are less abundantly provided.[17]

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

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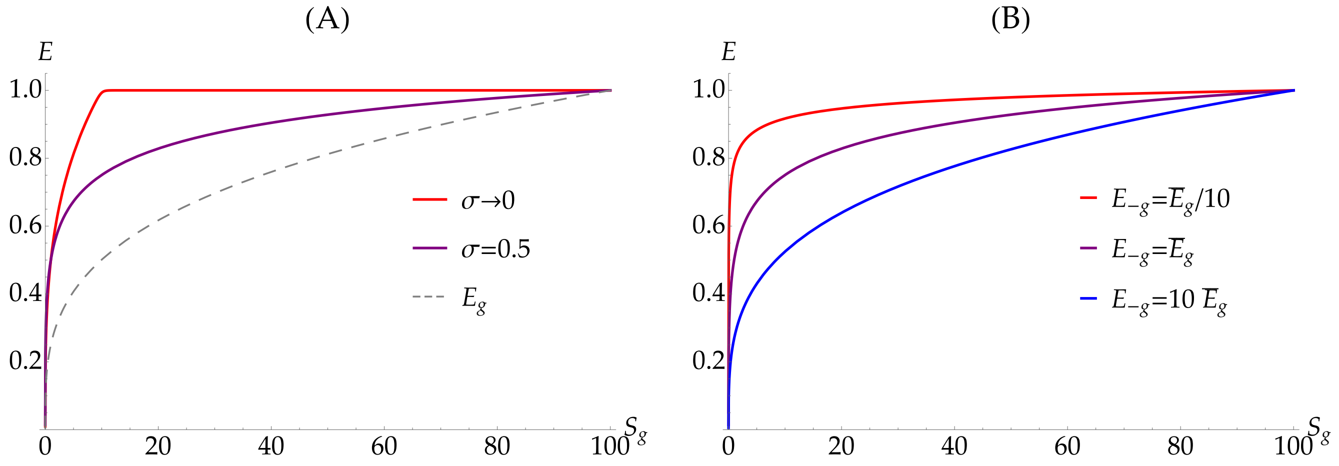
[17] The prediction that the effect of species loss in function group g on the overall ecosystem depends on its relative abundance E_g/E is consistent with evidence in the ecology literature that increased resource availability (coming, for example, from a higher output of other functions) often leads to larger effects of species richness in function g on productivity (Hooper et al., 2005). For example, experimental work by He, Bazzaz and Schmid (2002) finds that *"at the low nutrient level, species richness did not have a significant effect on community productivity. However, at the high nutrient level, the community biomass decreased with decreasing species richness."* In a separate experiment, Fridley (2002) found that *"sown species diversity had little effect on production in plots of low fertility, but species-rich plots were twice as productive as monoculture plots at high fertility."* Similarly, Eisenhauer, Reich and Isbell (2012) found that plant diversity had larger effects on productivity in the presence of certain productive decomposers. In other words, when the ecosystem service "maintenance of soil fertility" was more abundantly provided (and soil fertility thus became less of a constraining force), changes in biodiversity (and therefore changes in the output) in a complementary function had a larger effect on overall ecosystem productivity.

Figure 3: Ecosystem Service Production and Biodiversity



Note: Panel A shows E and E_g as functions of S_g for two values of σ, with $\bar{E}_{-g} = \bar{E}_g$ and $S_{-g} = 10$, normalizing $E = 1$ when $S_g = \bar{S}_g$. Panel B shows E as a function of S_g for different values of E_{-g}, fixing $\sigma = 0.5$ and normalizing $E = 1$ when $S_g = \bar{S}_g$. In both panels, $\bar{S}_g = \bar{S}_{-g} = 100$, $\phi_g = 0.3$.

to substitute across functions in the production of aggregate ecosystem services. Consistent with this model implication, there is compelling empirical evidence that past losses of keystone species have had substantial ecological and economic effects. For example, Frank and Sudarshan (2023) find large-scale social costs from the collapse of the vulture population in India, which led, among other things, to a 4% increase in mortality due to the decline in sanitation services. The authors point out that in the ecosystem under investigation, vultures were without a *"good functional replacement in the ecosystem."*

More generally, Proposition 1 highlights that the effect on ecosystem productivity of losing a species is context-dependent: losing a species in a group that constrains overall ecosystem output and where there is little remaining functional redundancy can have large effects while losing a species in the same ecosystem in a group with more remaining functionally similar species (or one that does not constrain aggregate ecosystem productivity) has much smaller effects. This result aligns closely with findings from the empirical ecology literature, summarized by Hooper et al. (2005) as: "*ecosystem response to extinction or invasion in the real world will be determined at least as much by which species and functional traits are lost and remain behind as by how many species are lost. [...].*"[18] The relative impact of species loss in two functions g and h on ecosystem services and output can be formally captured by the marginal rate of

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[18] It is also consistent with the ecological fact that the designation of 'keystone species' is not a constant trait of a particular species, but is instead also context dependent. As explained by Power et al. (1996): *"The more species that are trophically similar to a species in the food web (or functionally similar to a species in the interaction web), the greater the chance that deleting that species would cause compensatory increases in species functionally similar to it [...]. This argument suggests that loss of species diversity may thrust more of the remaining species into keystone roles."* A popular analogy is that of the children's game "Jenga" in which players take turns removing a block at a time from a tower. Similar to our setting here, the importance of each remaining block for the overall stability of the tower depends on which other blocks have already been removed.

substitution (MRS) between these functions $\text{MRS}_{g,h} = \frac{\partial E/\partial S_g}{\partial E/\partial S_h}$, which takes the simple form:

$$\text{MRS}_{g,h} = \overline{\text{MRS}}_{g,h} \frac{s_g^{-\left[1+\phi_g\left(\frac{1}{\sigma}-1\right)\right]}}{s_h^{-\left[1+\phi_h\left(\frac{1}{\sigma}-1\right)\right]}}. \tag{13}$$

where $\overline{\text{MRS}}_{g,h}$ is the marginal rate of substitution absent biodiversity loss in functions g and h, i.e., when $s_g = s_h = 1$ (for instance capturing differences $a_g \neq a_h$). Equation (13) describes the relative loss of aggregate ecosystem output from losing species across two different functional groups. The two sources of concavity in the model, captured by $\phi < 1$ and $\sigma < 1$, interact to determine the criticality of different functions: for example, a lower σ increases the complementarity across functions and thus amplifies any differences in scarcity between functions.

Connection to Weitzman (1998)'s *Noah's Ark*. Our model connects to a seminal study by Weitzman (1998), who analyzed how to prioritize species when preservation is costly (see also Weitzman, 1992, 1993; Metrick and Weitzman, 1998). Holding preservation costs fixed, Weitzman (1998) proposes to rank species i 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 $j \neq i$. 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 to decompose $R_{i,g} = U_{i,g} + D_{i,g}$ where distinctiveness is given by:

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

and we omit a term $\frac{1}{\sigma} \log E$ that is common to all species. A species is more distinctive if it belongs to a function with higher v_g (lower substitutability ϵ_g) and lower s_g. A lower σ increases distinctiveness, and more so for species in functions with low s_g and high v_g. Relative to Weitzman (1998), this notion of distinctiveness focuses on species' contributions to ecosystem services, instead of its genetic content per se, consistent with arguments in Brock and Xepapadeas (2003) and Polasky, Solow and Broadus (1993) that the economic value of diversity need not be related to genetic diversity. Useful features of our framework are that it can be mapped directly to standard economic objects measuring substitutability and complementarity, and that it allows for tractable aggregation, as we demonstrate next.

2.2 Biodiversity Shocks and the Fragility of Ecosystem Services

Proposition 1 provides comparative statics to illustrate the highly non-linear effect of species loss on ecosystem services, focusing on species loss in a single function. Next, we build on this work to characterize how the aggregate impact of an arbitrary distribution of species losses across functions depends on the current, multi-dimensional, state of biodiversity. Throughout this section, we simplify expressions by assuming that $\bar{n}_g$ and $\bar{S}_g$ are the same across functions. We denote the covariance of two variables $\boldsymbol{x} = \{x_g\}$ and $\boldsymbol{y} = \{y_g\}$ across functional groups by $\text{Cov}(x, y) = \sum_g (x_g - \frac{1}{G}\sum_j x_j)(y_g - \frac{1}{G}\sum_j y_j)$.

We next decompose the aggregate effect of a distribution of shocks to species s_g into three conceptually distinct parts; in the Appendix, we extend this result to allow for shocks to $\bar{n}_g$.

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:*

$$d\log E = \underbrace{\sum_{g=1}^{G} \omega_g \frac{\alpha_g}{s_g} ds_g}_{\Delta\, \textit{Community abundance}} \quad + \quad \underbrace{\sum_{g=1}^{G} \omega_g \frac{v_g}{s_g} ds_g}_{\Delta\, \textit{Within-function niche differentiation}} \quad + \quad \underbrace{Cov\left[\gamma_g, \frac{\phi_g}{s_g} ds_g\right]}_{\Delta\, \textit{Across-function imbalances in biodiversity}} \quad , \tag{14}$$

where $v_g = 1/(\epsilon_g - 1)$ captures the returns to within-function biodiversity through niche differentiation, and $N_g = \sum_{i=1}^{S_g} n_{i,g}$ captures the total population in function g, and we denote:

$$\omega_g = \frac{N_g}{\sum_{j=1}^{g} N_j} \qquad \textit{(population/abundance share)},$$

$$\mu_g = \frac{s_g^{\phi_g \frac{\sigma-1}{\sigma}}}{\sum_{j=1}^{G} s_j^{\phi_g \frac{\sigma-1}{\sigma}}} \qquad \textit{(criticality)},$$

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

The weights ω_g are the abundance shares of each function and thus sum to 1. They do not depend on elasticities of substitution (σ or ϵ_g) and, all else equal, function g's population share increases with s_g.

The weights μ_g also sum to 1 and measure the *criticality* of different functions, with the relative criticality of two functions g, h related to the marginal rate of substitution between two species in these functions, defined in Section 2.1 ($\mu_g/\mu_h = s_h/s_g \times \text{MRS}_{g,h}$). All else equal, function g's criticality μ_g is decreasing in s_g, and 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. In addition, higher complementarity across functions (lower σ) amplifies the differences in criticality between functions induced by differences in s and ϕ_g.

Finally, the criticality-abundance gap, or simply gap, $\gamma_g = \mu_g - \omega_g$ captures the difference between function g's criticality and its population share; thus it is positive if and only if function g is critical relative to its population share, which can happen because within-function returns to biodiversity v_g are relatively high or s_g is particularly low. The gaps γ_g always sum to 0, and, in general, some are positive and some negative. They are all equal to 0 only in the case of uniform past biodiversity losses ($s_g = s$ for all g). A lower σ contributes to gaps that are larger in absolute magnitude.

Decomposing the Effects of Biodiversity Loss. Proposition 2 shows that the total effect of a given species loss on the production of ecosystem service can be decomposed into three distinct channels. The most obvious effect is the change in community abundance captured by the first term in equation (14):

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

which is equal to $d \log(\sum_{g=1}^{G} N_g)$. Species loss leads to a decline in the total mass of “producers," thereby reducing total ecosystem service production. Crucially, this size effect is unrelated to bio*diversity*, and would be present even if ecosystem services were produced by a single, homogeneous, species, or equivalently, if all species across all functions were perfectly substitutable (i.e., if $\epsilon_g = \sigma = \infty$).[19]

By contrast, the other terms in equation (14) can be non-zero only if there is a value of biodiversity in the sense that not all species and functions are perfect substitutes. In this case, the precise distribution of biodiversity losses across functions matters. The second term

$$\sum_{g=1}^{G} \frac{\omega_g}{s_g} v_g ds_g$$

denotes the change in within-function gains from biodiversity due to the niche differentiation effects discussed in Section 1.2.1. This term is equal to zero if $\epsilon_g \to \infty$ for all g, that is, if species are perfect substitutes within each function. With heterogeneity across functions, the effects depend on the distribution of past species loss: when biodiversity in a function has been depleted more—and we are thus on a steeper part of the concave within-function biodiversity-productivity relationship—further biodiversity losses in that function have larger effects on ecosystem productivity, in particular for functions with higher returns to biodiversity (corresponding to less substitutability across species).

The final term captures how *imbalances in biodiversity* across functions are affected by the shocks $\boldsymbol{ds}$:

$$\text{Cov}\left[\gamma_g, \frac{\phi_g}{s_g} ds_g\right]. \tag{15}$$

This covariance term is equal to zero if biodiversity losses occur around a symmetric initial allocation of biodiversity ($s_g = s$), in which case $\gamma_g = 0$. If instead there are pre-existing imbalances in s_g and the initial allocation of species was thus ’inefficient,’ the covariance term can be non-zero.[20] In this case, the covariance term captures how the new biodiversity shocks $\boldsymbol{ds}$ affect the imbalances in biodiversity due to past losses, measured by the criticality-abundance gaps γ_g. New biodiversity losses have stronger effects, i.e., $\text{Cov}\left[\gamma_g, \frac{\phi_g}{s_g} ds_g\right] > 0$, when they disproportionately hit functions with a higher gap, as the new

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

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

losses then amplify the pre-existing imbalances in biodiversity across functions. Conversely, the losses induce smaller reductions in ecosystem services, i.e., $\text{Cov}\left[\gamma_g, \frac{\phi_g}{s_g} ds_g\right] < 0$, if they occur in functions that are less critical relative to their abundance.

The Fragility of Ecosystem Services. A special case of the general specification of shocks to biodiversity ds_g considered in Proposition 2 is that of common shocks, defined as shocks that are either the same for all functions, or idiosyncratic but ex ante distributed identically across functions. Focusing on these shocks allows us to introduce the notion of *fragility of ecosystem services*.

Proposition 3. *Define the fragility of ecosystem services, or simply fragility, as:*

$$\mathcal{F}(\boldsymbol{s}) = \sum_{g=1}^{G} \mu_g \frac{\phi_g}{s_g}. \tag{16}$$

Then the impact of a common shock $ds_g = ds$ is:[21]

$$\begin{aligned} d\log E &= \mathcal{F}(\boldsymbol{s})ds. \\ &= \underbrace{\sum_{g=1}^{G} \omega_g \frac{\alpha_g}{s_g} ds}_{\Delta \textit{Community abundance}} + \underbrace{\sum_{g=1}^{G} \omega_g \frac{v_g}{s_g} ds}_{\Delta \textit{Within-function niche differentiation}} + \underbrace{Cov\left[\gamma_g, \frac{\phi_g}{s_g} ds\right]}_{\Delta \textit{Across-function imbalances in biodiversity}} \end{aligned} \tag{17}$$

Similarly, a uniformly distributed idiosyncratic shock with mean $d\bar{z}$, i.e., such that $dz_g = G d\bar{z}$ with probability $1/G$ and 0 otherwise for each g, has an expected impact

$$\mathbb{E}\left[d\log E | \boldsymbol{s}\right] = \mathcal{F}(\boldsymbol{s}) d\bar{z}.$$

In other words, the fragility $\mathcal{F}(\boldsymbol{s})$ of an ecosystem with biodiversity $\boldsymbol{s}$ captures the decline in the production of aggregate ecosystem services that would arise from a common shock ds across all functions and is determined by the three forces identified in Proposition 2.

As an example, consider the case of two functions ($G = 2$), with $\phi_1 = \phi_2 = \phi$ and potentially different outstanding levels of biodiversity $s_1 \leq s_2$. To focus on cross-functional effects in this example, we abstract from within-function niche differentiation and let $\epsilon_g \to \infty$ and thus $v_g \to 0$. Then

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

Both terms are always positive, with the second term equal to zero if and only if $s_1 = s_2$. In other words, imbalances always increase ecosystem fragility and thus add to overall loss of ecosystem services in

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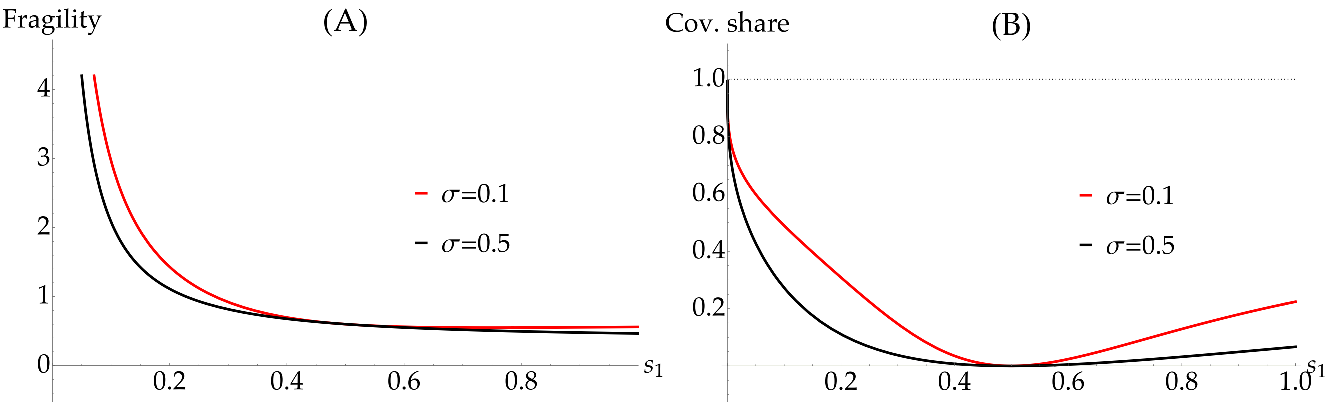
[21] While the expression in equation (14) could be equivalently expressed in terms of proportional shocks $d\log s_g = ds_g/s_g$, it is more common in the ecology literature to study how ecosystems are affected by shocks to the absolute number of species.

response to a common shock (the possibility for the covariance term to reduce overall ecosystem loss was dependent on the possibility that asymmetric species loss might only hit less depleted functions): a decrease in s_1 and corresponding increase in s_2 that leaves total abundance unchanged but further increases the dispersion in s increases imbalances and therefore fragility.

Panel A of Figure 4 shows $\mathcal{F}$ as a function of s_1, holding s_2 fixed at 0.5. $\mathcal{F}$ is positive throughout and unambiguously rises as s_1 falls below s_2. In the region $s_1 > s_2$ there are two counterveiling forces: on the one hand, a higher s_1 has a mechanical positive impact on total abundance $N_1 + N_2$, which reduces fragility, while on the other hand it increases dispersion in s and thus the term due to imbalances; the net effect of a higher s_1 is always a reduction in fragility. More complementarities across functions (lower σ) amplifies the fragility of ecosystem services for any value of s_1. Panel B shows the resulting covariance share in fragility $\mathcal{F}$ as a function of s_1, again holding s_2 fixed at 0.5. The share of ecosytem fragility due to misallocation goes to 1 as $s_1 \to 0$ holding s_2 fixed: $\lim_{s_1 \to 0} \frac{1}{\mathcal{F}(\boldsymbol{s})} \mathrm{Cov}\left[\gamma_g(\boldsymbol{s}), \frac{\phi_g}{s_g}\right] = 1$.

Figure 4: The Fragility of Ecosystem Services.



Note: Panel (A) shows $\mathcal{F}$ as a function of s_1, fixing $s_2 = 0.5$. Panel (B) shows the share of fragility coming from misallocation $\mathrm{Cov}\left[\gamma_g, \frac{\phi_g}{s_g}\right] / \mathcal{F}$, as a function of s_1, fixing $s_2 = 0.5$. $\phi = 0.3$ for both $g = 1, 2$.

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.

Proposition 4. *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.*[22] *Then:*

(i) The expected effect of a date-t species loss shock on ecosystem service production, normalized by $-\delta$, is given by

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[22] 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 $N(t) = N(0) - \delta t$.

the expected fragility at date t, and is increasing over time.

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

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

$$BR(t) = \frac{1}{\delta}\sqrt{\mathbb{E}_0\left[Var(d\log E(t))\right]} \tag{18}$$

$$= \sqrt{\mathbb{E}_0\left[Var(\mathcal{F}(\boldsymbol{s}(t)))\right]} \tag{19}$$

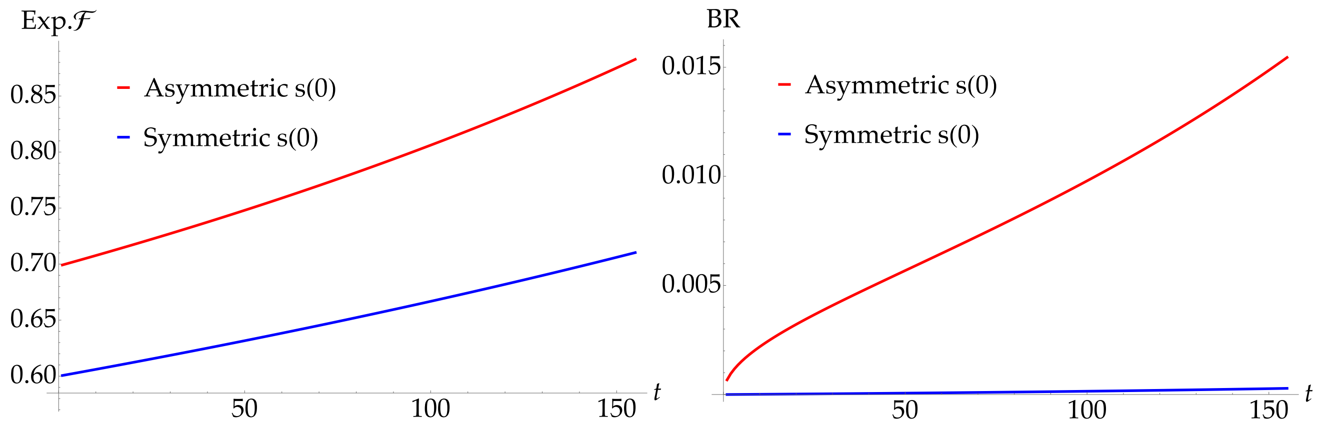
Part (i) of Proposition 4 states that expected fragility increases over time. This is driven by the three forces described in equation (17): the average number of species s_g falls in all functions, which increases both $\sum_{g=1}^{G}\omega_g\frac{\alpha_g}{s_g}$ and $\sum_{g=1}^{G}\omega_g\frac{v_g}{s_g}$, and imbalances in biodiversity are expected to rise simply because some functional groups will randomly face larger species losses than others. Even though we assume that the shocks follow a stationary process (i.e., the number of species lost in each period remains stable), the depletion of natural capital makes the ecosystem more sensitive to the same shocks as time unfolds.

Part (ii) of Proposition 4 shows that the increased fragility also translates into an increasing expected range of potential effects on ecosystem service provision from a given species loss, as measured by the a larger expected dispersion in the response to shocks $d\log E(t)$. Thus *biodiversity risk*, expressed in terms of the risk to ecosystem services production, is expected to rise over time even when holding the process of species loss fixed. Intuitively, at any point in time, the best case scenario happens if species loss is concentrated in functions with relatively high biodiversity, as then the realized aggregate effect can be smaller than implied by the total loss in biomass. Conversely, the worst case scenario is when a shock hits a function that already features low biodiversity. As time unfolds, the difference between the best and worst outcomes following a given shock are expected to increase. Note that BR(t) as defined in equation (19) is a measure of *forward* risk, i.e., the expected dispersion of $d\log E(t)$, and not the expected dispersion in $E(t)$ itself, which would capture a *cumulative* risk that would rise over time even in a world without any role for biodiversity (i.e., such that $\sigma, \epsilon_g \to \infty$), simply through the accumulation of shocks.

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

Summary. Our model yields a tractable measure of the fragility of ecosystem services and how it is affected by species loss over time. Ecosystem fragility captures three conceptually distinct ways in which species loss affects ecosystem services production: (i) a direct reduction in community abundance (i.e.,

Figure 5: Fragility and Biodiversity Risk over Time.



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

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

2.3 Implications for Policy Makers and Beyond

Our expositions of the production function of ecosystem services and the fragility of ecosystems have important implications for several ongoing policy debates, which we briefly discuss here.

Interpreting Economic Effects of Past Biodiversity Loss. First, our model highlights the problems with one of the most tempting (and most common) attempts to dismiss the potential importance of biodiversity loss for economic activity: the fact that it is not easy to tell compelling narratives of how the dramatic loss of biodiversity over the past decades has led to large-scale declines in economic output.[23] A skeptic might say: *"It's hard for me to worry about biodiversity loss from an economic perspective if you cannot tell me clear stories of how output today would be substantially higher if it weren't for the large recent decline in biodiversity."*[24] While it is always possible to point to a few well-identified studies that were

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[23] This is in contrast to discussions of the economic effects of climate change, where the economic and financial damages from already occuring sea levels, wildfires, hurricanes and extreme heat are more immediately measurable, leading to an increased appreciation of physical climate risks (Giglio, Kelly and Stroebel, 2021; Giglio et al., 2021; Stroebel and Wurgler, 2021).

[24] This problem is particularly acute since the most popular (and vivid) such narrative links the loss of pollinators to declines in agricultural productivity. And yet, despite the observed decline in pollinator abundance and diversity, agricultural productivity has substantially increased in recent decades (IPBES, 2019). While an astute empiricist would point out that such productivity might have grown even more in a counterfactual without pollinator loss—a claim buffeted by findings that crops with greater pollinator dependence had lower yield growth over the past decades (Garibaldi et al., 2011)—the difficulty of constructing such a counterfactual quickly blunts the effectiveness of this narrative in convincing a skeptical listener.

able to link the loss of particular species to meaningful economic losses—for example, the economic losses from the extinctions of vultures in India documented by Frank and Sudarshan (2023)—our model highlights two additional compelling responses. First, not all biodiversity loss is the same in terms of its economic effects, and the lack of economic effects of biodiversity loss in some ecosystems does not mean such losses will have small effects everywhere. And second, a key effect of past losses of biodiversity is to have increased ecosystem fragility $\mathcal{F}$ such that any *future* losses of biodiversity will have increasingly large economic effects. Prudent policymakers aware of these non-linearities might want to act well before the effects of biodiversity loss materialize in meaningful present-day economic losses.

Pigovian Taxes and the Prioritization of Conservation Activities. Policymakers hoping to protect biodiversity have a number of options such as introducing Pigovian taxes on activities that threaten biodiversity or declaring conservation areas that limit economic activities. The heterogeneity in the marginal economic values of different species highlights that the economic gains from such regulations can be maximized by targeting taxes and conservation efforts towards species loss in those functions with little remaining redundancy, as well as those functions whose current output is binding for overall ecosystem productivity. In Section 3.4, we provide a formal analysis of the optimal conservation problem across multiple functions and locations. Intuitively, 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. As discussed, this identification of the economically most meaningful conservation efforts requires a collaboration between economists and ecologists (see Oliver et al., 2015, for an example of a helpful analysis of ecosystem function health), and our general organizing framework can guide those collaborations.

Biodiversity Offsets. In many settings, it might not be possible to fully eliminate the negative effects of certain economic activities on local ecosystems. In those cases, many regulatory regimes have a role for "biodiversity offsets," defined by Carbon Brief as "conservation activities intended to compensate for the lasting impacts of development on species and ecosystems that persist even after other mitigation measures."[25] A key principle of biodiversity offsets is that they should lead to a "no net loss" outcome. Our findings highlight the importance of specifying the exact metric for 'no net loss' given that 'no net loss of species' does not generally translate into a 'no net loss for ecosystem functioning.' Our MRS between different species provide a framework to guide what conservation activities should be required to offset a certain ecosystem loss.

Measuring Economic Risk from Biodiversity Loss. In recent years, regulators around the world have started to assess the exposure of their local economies and financial systems to risks from biodiversity loss. To guide such assessments, the OECD (2023) has provided a *Supervisory Framework for Assessing Nature-Related Financial Risks*, and the NGFS (2023) has begun the process of developing biodiversity

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[25] There is a similar efforts to construct a system of "carbon offsets" which involve activities that reduce the amount of carbon in the atmosphere relative to a counterfactural (e.g., due to reduced deforestation or efforts at reforestation). While such carbon offsets face many challenges to ensure the additionality of any actions, they are easier to implement, since they can rely on "a ton of carbon" as a common unit of account to measure the effects on climate change.

risk scenarios that could be used in biodiversity stress tests (see Acharya et al., 2023, for a related discussion of climate stress tests). Much of the existing work has focused on identifying those sectors of the economy that most directly depend on ecosystem services, and that might therefore be most affected by nature-related losses. Combined with information of the exposure of financial institutions to those sectors, researchers have produced first proxies for the biodiversity risk exposure of the financial system (van Toor et al., 2020; Svartzman et al., 2021; Bank Negara Malaysia, 2022; Boldrini et al., 2023). Our framework might help advance this work towards a more complete risk assessment, which traditionally involves a consideration of hazards and vulnerabilities in addition to exposures (NGFS, 2023). The evaluation of hazards in particular requires identifying which ecosystem services are most at risk from reasonable forecasts of further species loss.[26] Realizing that *"the magnitude and likelihood of shocks caused by nature depletion are important,"* Boldrini et al. (2023) go furthest towards providing a more complete risk analysis. Specifically, they consider biodiversity shocks from changes in 'mean species abundance' in different geographies between 2015 and 2050 as forecast by the GLOBIO model (Schipper et al., 2020). Our specification of ecosystem service fragility highlights that the overall economic risks from such changes in mean species abundance depend also on the current state of ecosystems, including on whether there are any asymmetries in ecosystem depletion across functions. Our work can thus provide a structure to think about further developments of the relevant risk frameworks.

3 Biodiversity and the Economy

In this section we study the two-way interactions between biodiversity and economic activity. We start by specifying an aggregate production function that includes physical capital, land use, and ecosystem services, similar to equation (1). We then introduce a simple process that describes the dynamics of both species abundance and biodiversity, and describe how economic activity affects those processes. We conclude by studying, in a stylized setting, 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 base our specification of the production function in equation (1) on two main insights from the ecology literature. The first one follows from the "strong sustainability" concept proposed by Dietz and Neumayer (2007) and Ekins et al. (2003), which highlights the difficulties of substituting for several key ecosystem services by increasing other factors of production. This insight was core to the influential Dasgupta (2021) Review, which concluded that there is *"little-to-no substitution possibilities between key*

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[26] The NGFS (2023) proposes the use of the ESGAP "Strong Environmental Sustainability Index"—a measure of identifying the distance between the current state and a health state for different ecosystems—to provide such an analysis. We agree that this metric seems a reasonable starting point for the identification of relatively vulnerable ecosystems. Other promising metrics are those produced by the InVEST framework, a *"spatially explicit modeling tool to predict ecosystem services, biodiversity conservation and commodity production levels"* (Nelson et al., 2009).

forms of natural capital and produced capital, or for that matter any other form of capital."[27] As a consequence, minimum levels of ecosystem services must be maintained to sustain economic activity and human life more broadly (see also Cohen, Hepburn and Teytelboym, 2019).[28]

The second insight is that the use of natural resources, while potentially destructive for biodiversity, provides economic benefits by increasing output today. For example, key drivers of biodiversity loss are land use changes that redirect land towards the production of economic output instead of leaving it to nature to produce ecosystem services (see, for example, IPBES, 2019; Johnson et al., 2021). To capture such mechanisms, we directly include land as another factor of production in equation (20). We refer to L as the (fixed) amount of land available, and choice variable $u \in [0, 1]$ as the fraction of land used for economic production, so that $1 - u$ is the land that is left to nature. In Section 3.2, we then specify the process through which increases in u lead to reductions in natural capital and biodiversity.

Economic Production Function. Integrating these insights generates the following economic production function, which could easily be expanded to include labor and other factors of production with different degrees of complementarity or substitutability:

$$F(K, E, uL) = \left(\left[K^{\theta} (uL)^{1-\theta} \right]^{\frac{\xi-1}{\xi}} + a_E E^{\frac{\xi-1}{\xi}} \right)^{\frac{\xi}{\xi-1}}. \tag{20}$$

Ecosystem services and a composite of capital and land are assumed to have equal shares for illustrative purposes, while θ is the share of capital among the other factors. "Strong sustainability" is captured by an elasticity of substitution $\xi \leq 1$ between ecosystem services and the other factors of production.

Several interesting implications emerge directly from the assumption of complementarity between (composite) capital and ecosystem services. To highlight this complementarity, we refer to composite capital as $\tilde{K} = K^{\theta}(uL)^{1-\theta}$, and rewrite the function as $F(\tilde{K}, E) = \left(\tilde{K}^{\xi-1/\xi} + a_E E^{\xi-1/\xi} \right)^{\xi/\xi-1}$. We also scale the output at a certain level E by the output that would be obtained with the same capital $\tilde{K}$ with maximal

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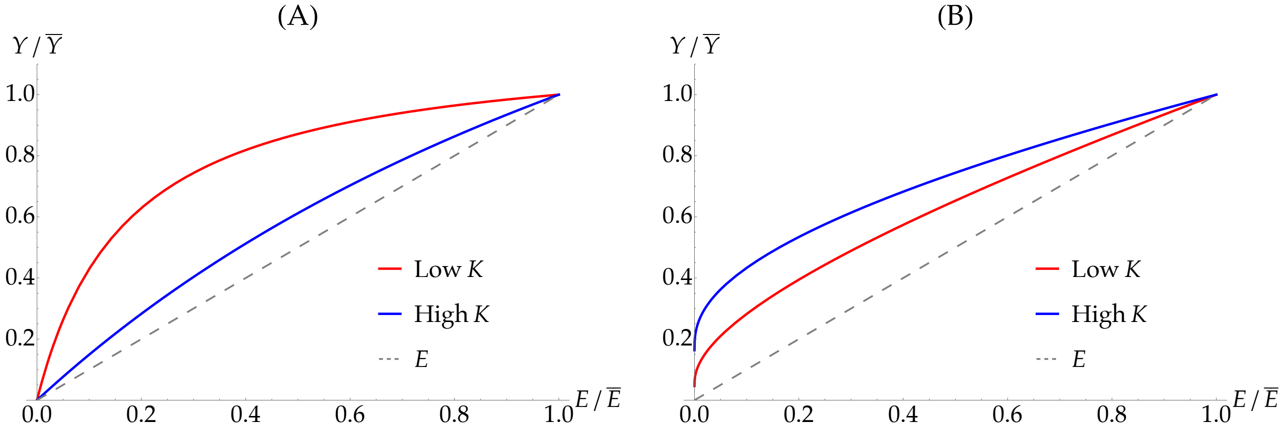
[27] In a lengthy review of the substitutability of ecosystem services and other factors of production, Ayres (2007) similarly comments that *"the surprise, for me, in writing this paper is the extent to which the biosphere embodies a fundamental natural technology for which there is no known (or likely)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

[28] One implication of the complementary of ecosystem services with other factors of production is that any attempt to value the overall contribution of ecosystem services to economic activity is highly difficult, and would not be achievable by looking at their contribution to GDP. As Dasgupta (2021) highlights: *"pollinators may be of great value even if their measurable services to GDP are of negligible worth."* This mirrors similar challenges that an economist would face who would conclude that, since energy's share in GDP was only a few percentage points, we would not see a large scale economic collapse if the economy was to suddenly need to run without energy. Given these challenges, we believe that most effort to value "natural capital" are conceptually flawed—since the value of each ecosystem services is so highly context dependent—and we instead choose to focus on understanding the effects of *marginal* changes in biodiversity on economic output.

Figure 6: Ecosystem Services, Capital, and Output



ecosystem services $\bar{E}$ (i.e., without any biodiversity loss), and refer to this as normalized output, F^{norm}.

$$F^{norm}(\tilde{K}, E) = \frac{F(\tilde{K}, E)}{F(\tilde{K}, \overline{E})} \tag{21}$$

Consider an economy with a fixed level of composite capital $\tilde{K}$, and imagine varying the use of ecosystem services, E. If $E = 0$, $F^{norm}(\tilde{K}, E) = 0$, and the economy produces no output. If $E = \overline{E}$, $F^{norm}(\tilde{K}, E) = 1$, and the economy produces the maximum possible output available for that amount of capital $\tilde{K}$. An intermediate choice of E will produce intermediate values of normalized output in a way that depends directly on the degree of complementarity between these factors of production.

Consider first the case in which $\xi < 1$ as shown in Panel A of Figure 6, which plots $F^{norm}(\tilde{K}, E)$ as a function of $E/\bar{E}$ between 0 and 1, separately for a low-capital and a high-capital economy. Since ecosystem services are a useful factor of production, output increases with E. In a capital-rich economy (blue), ecosystem services tend to be the constraining factor. Adding ecosystem services is useful, and this usefulness—corresponding to the marginal productivity of E given by the slope of the line—remains high even as more of E is added: the normalized output is close to flat as a function of E. In a low-capital economy (red), in which capital is the constraining factor, the usefulness of E for production (the marginal productivity) declines quickly. Ecosystem services are very valuable for production only when E is sufficiently low that it effectively is the constraining factor. But because the economy has low levels of capital, adding more E quickly becomes less useful, and its marginal productivity (the slope of the red line) drops dramatically as E increases. In other words, the complementarity between capital and E induces a stronger concavity in this relation for more capital-poor economies.

This example highlights a key insights: while neither capital-rich (developed) countries nor capital-poor (developing) countries will want to get to the point where $E = 0$, the marginal value of ecosystem services will be very different in the two cases. A developed country will see ecosystem services as the constraining factor of production, and will have greater incentives towards their conservation, compared to a developing country, that has a relative abundance of natural resources, and will therefore have greater incentives to exploit them and partly compensate for the lack of physical capital.

For completeness, Panel B of Figure 6 shows that the exact opposite (in terms of concavity of this relation) occurs if $\xi > 1$, i.e., when ecosystem services and capital are substitutes. Finally, note that while we have discussed these results through a specific calibration depicted in the figure, they are general properties of the production function (20). We return to these insights in the context of a calibrated model that directly accounts for the choice that economies have on the use of natural resources.

3.2 Economic Activity and the Dynamics of Biodiversity

Since ecosystem services and land use both enter the production function, the management of biodiversity is important to society. To understand the optimal decision to preserve biodiversity from an economic perspective, we next describe how the dynamics of biodiversity are affected by economic activity. We focus on the effect of economic activity on biodiversity through the use of land for economic production captured by the choice variable u. A higher use u—corresponding to a higher share of available land used for economic activity—puts pressure on the ecosystem, which can lead to an initial direct loss in biomass (e.g., through deforestation) as well as subsequent species loss, due to the fact that the ecosystem becomes more vulnerable to ecological shocks that can lead to extinction of some species.

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 expenditure for the conservation of natural capital). Given initial conditions $(K_0, \boldsymbol{s}_0)$, the country's planner chooses u and K_1 to maximize

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

where

$$\begin{aligned} C_0 &= F(K_0, uL, E_0) - K_1, \\ C_1 &= F(K_1, \bar{u}L, E_1(u)). \end{aligned}$$

For notational simplicity, we assume full depreciation of the initial capital stock K_0 (hence K_1 is given by the date-0 investment), and take long-run (date-1) land use $\bar{u}$ as given.[29]

Land use u increases production Y_0, but at a cost to future ecosystem services E_1. This cost come from two channels that capture 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"*. First, there is a direct impact of land use on overall abundance. For instance, deforestation reduces abundance within 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 $1 - u$. Second, land use negatively

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[29] Imposing a relation such as $\bar{u} = u$ would only complicate the marginal benefit of land use (incorporating both a present and future component) without meaningfully affecting the result. One interpretation is that we solve a problem without commitment, with $\bar{u}$ chosen by future generations and the current planner is "naive," a term borrowed from the hyperbolic discounting literature meaing that the current planner is not trying to affect future generations' choice of u through current policies.

affects biodiversity in function g according to the following reduced-form specification:

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

Biodiversity loss increases with land use, that is, the species loss function $\mathcal{L}$ is increasing in u. One interpretation is that as the abundance of each species declines due to land use, the risk of extinction increases. Indeed, the ecology literature has found that *"the smaller the population size of a particular species, the more likely it is to go extinct locally, due to random—stochastic—fluctuations"* (Cleland, 2011).

Biodiversity as an exhaustible resource. Our setup connects to the seminal literature on the optimal exhaustion of a depletable natural resource (Hotelling 1931, Dasgupta and Heal 1974, Solow 1974) but features three important differences. First and foremost, as we argued extensively, ecosystem service production has multiple complementary dimensions. Moreover, the effects of land use on these different functions cannot be easily disentangled. This is in stark constrast with the extraction of exhaustible resources such as fossil fuels, which are more likely to be substitutes, and whose extraction can be more finely targeted, for instance, by focusing on coal, oil, or gas depending on the respective outstanding stocks. We will show that, as a result, optimal land use is severely constrained by the weakest ecological functions, even though other functions may still be abundant.

Second, ecosystems affect production directly through a flow of ecosystem services in each period, whereas in the case of a standard exhaustible resource extraction, only the actual resource utilization in each period affects production. This means that biodiversity loss has a permanent and irreversible impact to reduce the productivity of ecosystems even after a country stops using land for economic production. While mean-reversion in biodiversity (e.g., new species appearing) that would allow ecosystem services to recover is possible, it is likely to occur at much longer horizons than what is relevant in our context. Hence, in our simple model, we consider species loss as permanent. By contrast, a lower stock of standard exhaustible resources only hurts economic productivity indirectly, by limiting how much of the resources can be extracted in the future.

Third, although in our baseline model we will assume a tractable species loss function $\mathcal{L}$ that is linear in land use to obtain analytical insights, in general the law of motion of biodiversity can be highly nonlinear and state-dependent. In particular, the cross-derivative $\frac{\partial^2 \mathcal{L}}{\partial u \partial s_{g,0}}$ can capture potential tipping points and selection effects that have no counterpart when thinking about standard exhaustible resources. 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 (i.e., the most fragile species disappear first).

Finally, the mapping between economic activity and future ecosystem services is not as tight as in the case of other exhaustible resources. Beyond the deterministic impact of economic activity on abundance and species loss, ecosystems also become less resilient to other shocks such as natural disasters and diseases, as we argued in Proposition 4. We focus here on a deterministic setting as a first step, but the presence of these other shocks would induce an additional precautionary motive for the conservation of natural capital, as preserving current species has the additional benefit of making ecosystems more robust to future random species losses.

Model Solution. Denote for any factor $X \in \{K, L, E\}$

$$\eta_{X,t} = \frac{\partial \log Y_t}{\partial \log X_t}$$

the elasticity of date-t output to X_t. In general these elasticities are endogenous objects that need to be determined as part of the optimal solution, except in the case of a Cobb-Douglas production function.

The optimality condition with respect to investment in physical capital K_1 can be expressed as an optimal savings rate:

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

As in a standard model without ecosystem services, optimal savings in physical capital increase with patience β and with the elasticity of date-1 output to capital K_1, $\eta_{K,1}$ (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 also express it as an optimal conservation rate $1 - u$ for natural capital. Any interior solution must satisfy:

$$1 - u = \Lambda \frac{\partial \log E_1}{\partial \log(1 - u)},$$

where we define

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

The reduced-form parameter Λ measures the cost of depleting future ecosystem services E_1 relative to the benefits from current land use. When Λ is high, the harmful effects of land use on abundance and biodiversity dominate.

Lemma 1. *Given the production function* $F(K, u, E) = \left[\left(K^{\theta} u^{1-\theta} \right)^{\frac{\xi - 1}{\xi}} + a_E E^{\frac{\xi-1}{\xi}} \right]^{\frac{\xi}{\xi - 1}}$ *we have*

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

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

Therefore Λ is increasing in the importance of ecosystem services for output a_E and in patience β – since the costs of depleting natural capital are borne in the future whereas land use has an immediate benefit. When the production function in equation (20) is Cobb-Douglas ($\xi = 1$), Λ is constant, equal to $\frac{\beta a_E}{1-\theta} \cdot \frac{1}{1 + (1+\beta\theta)/(1+a_E)}$. Otherwise, when $\xi < 1$, Λ increases with current land use u (since X_0 increases with u) and with the ratio of future capital K_1 over future ecosystem services E_1, consistent with our previous discussion.

We can further unpack the effect of land use on future ecosystem services into two terms, to obtain

$$1 - u = \underbrace{\Lambda}_{\text{direct abundance loss}} + \underbrace{(1-u)\Lambda \left[\sum_{g=1}^{G} \phi_g \frac{\mu_g(\boldsymbol{s}_1)}{s_{g,1}} \frac{\partial \mathcal{L}}{\partial u}(s_{g,0}, u) \right]}_{\text{biodiversity loss}}. \tag{23}$$

Conservation $1 - u$ increases future ecosystem services in two ways: the first term captures the direct effect on abundance holding biodiversity fixed, while the second term captures the effect on biodiversity through the species loss function $\mathcal{L}$, and captures, broadly speaking, an effect similar to productivity shifters on physical capital. If, in addition, land use has a simple linear effect on species loss (equal to δu), we can simplify the second term to

$$\sum_{g=1}^{G} \phi_g \frac{\mu_g(\boldsymbol{s}_1)}{s_{g,1}} \frac{\partial \mathcal{L}}{\partial u}(s_{g,0}, u) = \delta \mathcal{F}(\boldsymbol{s}_1)$$

where $\mathcal{F}$ is the fragility of ecosystem services defined in Proposition 3. This yields the following characterization:

Proposition 5. *The optimal conservation of natural capital satisfies*

$$1 - u = \min \left\{ 1, \frac{\Lambda}{1 - \Lambda \sum_{g=1}^{G} \phi_g \frac{\mu_g(\boldsymbol{s}_1)}{s_{g,1}} \frac{\partial \mathcal{L}}{\partial u}(s_{g,0}, u)} \right\}.$$

If in addition the species loss function is

$$\mathcal{L}(s_{g,0}, u) = \delta u \tag{24}$$

then

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

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

Comparative statics: *The optimal conservation $1 - u$ decreases with initial biodiversity $\boldsymbol{s}_0$ and 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 $\xi < 1$.*

Equation (23) provides an intuitive formula for the optimal conservation of nature $1 - u$. It increases with Λ and therefore with patience β, just like optimal investment in physical capital. This is true even absent any effect of land use on biodiversity ($\partial \mathcal{L} / \partial u = 0$). The second term in equation (23) highlights the role of biodiversity, and equation (25) shows that the optimal conservation of nature increases with fragility $\mathcal{F}$, which we showed is higher when some functions are already critical, with a low $s_{g,0}$.

At an abstract level, our framework can be viewed as a standard exhaustible resource problem when land use only affects abundance, with no impact on species loss (i.e., $\delta = 0$). In that case, the optimal conservation is simply given by Λ. In the presence of biodiversity loss $\delta > 0$, the optimal conservation

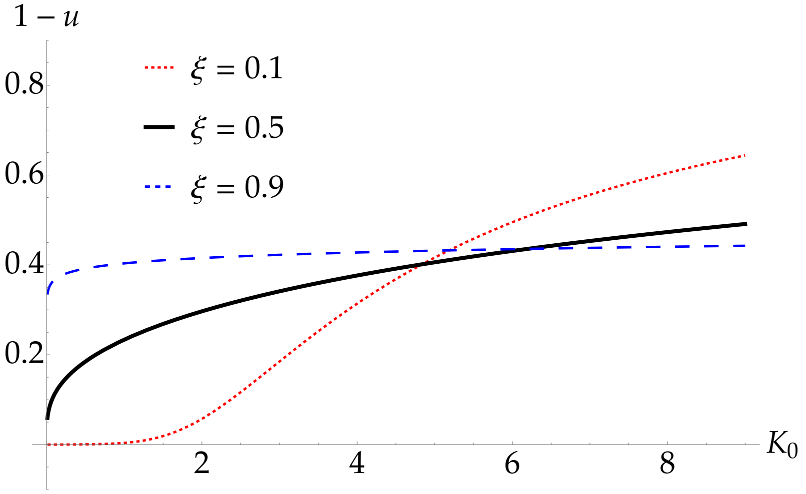

Figure 7: Optimal conservation $1-u$ as a function of initial capital stock K_0, for different values of ξ.

problem is much richer, but the optimal solution can be simply mapped to the notion of fragility previously defined. Effectively, biodiversity loss implies a marginal cost of depleting natural capital that increases sharply with past species loss and thus past land use. The effect depends endogenously on how functions interact to produce ecosystem services (through the parameter σ), and on the within-function gains from biodiversity, captured by the parameter ϕ_g.

The optimal conservation of natural capital decreases with initial biodiversity 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 cost of having depleted natural capital in the future relative to the current benefits from land use, and therefore with the importance of ecosystem services in production a_E and with patience β.

Most importantly, 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.[30] 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. Figure 7 illustrates this result. The baseline case, represented by the solid black line, corresponds to an elasticity $\xi = 0.5$ which captures a moderate complementarity between physical capital and ecosystem services. In this case the optimal conservation of natural capital $1-u$ increases smoothly with K_0. The two other lines illustrate what happens with a much higher elasticity $\xi = 0.9$ (blue dashed line), in which case the optimal conservation becomes less dependent of K_0 (and completely flat in the limit $\xi \to 1$), as well as a much lower elasticity $\xi = 0.1$ (red dotted line) in which case the optimal conservation becomes extremely low, i.e., land use is optimally very high, in capital-poor countries.

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[30] This is the case even with full depreciation of the initial stock K_0; the asymmetry between countries would be amplified with partial depreciation.

3.3 The role of across-function imbalances in biodiversity

A useful benchmark that can be solved in closed form (given Λ) is the case of symmetric initial biodiversity across functions, $s_{g,0} = s_0$ for all g. With that assumption, equation (25) simplifies to

$$1 - u = \frac{\Lambda}{1 - \frac{\Lambda\delta\phi}{s_0 - \delta u}}, \tag{26}$$

which is a quadratic equation in u with only one positive solution.

Our discussion of the fragility of ecosystem services in Section 2 shows that asymmetric past biodiversity losses create "imbalances" between functions, that increase the fragility of the ecosystem as a whole, thus calling for less land use, i.e., a higher conservation of natural capital $1 - u$. This is a key distinction between our framework and the standard model of optimal exhaustible resource extraction that focuses on a single resource. As long as land use and other damages from economic activity cannot be targeted towards the more abundant functions, the weakest functions impose a constraint on general land use even if other ecosystems are still intact (in Section 3.4 below we extend the model to allow for targeted land use and biodiversity offsets).

This principle can be illustrated most transparently in the limit case of no substitutability between functions ($\sigma \to 0$), which implies that fragility is entirely determined by the *most critical function:*

$$\mathcal{F}(\boldsymbol{s}) \to \frac{\phi}{\min_g s_g}.$$

As a result, optimal conservation is given by the same equation (26) as in the case with symmetric biodiversity $s_{g,0} = s_0$, but using $\underline{s}_{g,0} = \min_g s_{g,0}$ instead of the common s_0.[31]

Proposition 6. *Suppose that $\phi_g = \phi$ for all g and species loss follows equation (24). With symmetric biodiversity across functions ($s_{0,g} = s_0$ for all g), the optimal conservation of natural capital satisfies*

$$1 - u = \left[s_0 - \delta\left(1 + \Lambda(1+\phi)\right)\right] \frac{\sqrt{1 + \frac{4\Lambda\delta(s_0 - \delta)}{[s_0 - \delta(1+\Lambda(1+\phi))]^2}} - 1}{2\delta}. \tag{27}$$

With asymmetric biodiversity across functions and in the limit of no substitutability between functions $\sigma \to 0$, the optimal conservation of natural capital satisfies

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

where

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

is the most critical ecosystem function.

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[31] This result is reminiscent of the "O-ring theory" (Kremer, 1993) stating that a complex production process featuring complementarity between specialized units is only as strong as its weakest part.

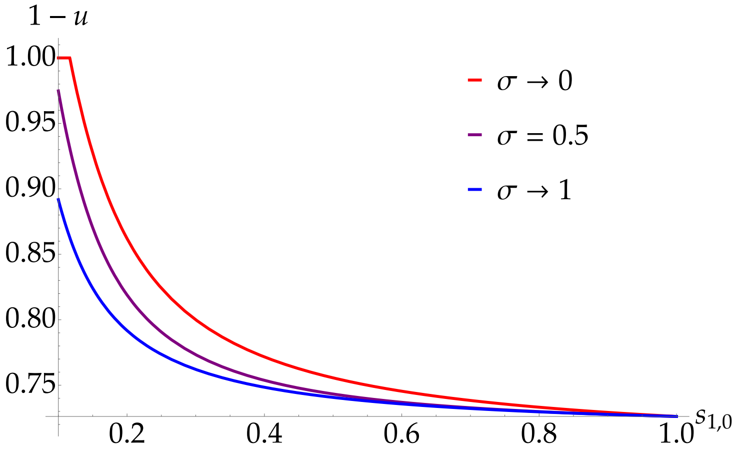

Figure 8: Optimal conservation $1-u$ as a function of $s_{1,0}$ for different values of σ.

For intermediate values of σ, Figure 8 shows, in an example with two functions, how σ affects the optimal conservation $1-u$ as a function of the imbalances between functions. Here $s_{2,0}$ is kept at 1 and we only vary $s_{1,0}$. The optimum with both functions equal to $s_{2,0} = s_{1,0}$ gives an upper bound for the optimal conservation, and for lower values of σ the actual optimum gets closer to this upper bound.

3.4 Targeted land use

We argued that one 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 and 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 7. *The vector of optimal conservation across functions satisfies*

$$\frac{1}{\sum_g \frac{\mu_g(\boldsymbol{s}_1)}{1-u_g}} = \frac{\Lambda}{1-\Lambda\delta\mathcal{F}(\boldsymbol{s}_1)}. \tag{28}$$

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

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

Equation (28) is the counterpart of equation (25) in Proposition 5, but applied to the (harmonic) average of optimal conservation levels across functions $\frac{1}{\sum_g \mu_g(\boldsymbol{s}_1)/1-u_g}$, weighted by each function's criticality μ_g.

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 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 intuitive direction: scarcer functions should be more preserved. The design of Pigovian policies towards the conservation of natural capital should thus take into account past biodiversity loss for two reasons: first, the relative impact of land use on abundance loss (holding future biodiversity $\boldsymbol{s}_1$ fixed) depends on the criticality of each functions, and second, functions that are already critical must be protected even more once we take into account how land use affects species loss.

3.5 Summary of Key Implications

In this section we modeled the two-way feedback between ecosystem services and the economy. Natural capital benefits economic production by providing a flow of ecosystem services. Under the "strong sustainability" hypothesis, there is limited substitutability between standard factors of production and ecosystem services. Conversely, economic activity such as land use harms ecosystems through a direct loss in abundance (e.g., deforestation that reduces biomass across all species) and biodiversity loss (i.e., a reduction in the number of species due to the rise in extinction risk at lower abundance).

We derive how each country should balance the current economic benefits from land use against the future economic costs owing to the depletion of ecosystems. Our model generalizes the classic analysis of the extraction of exhaustible resources to the multi-dimensional setting required in the context of biodiversity. The optimal conservation increases with the fragility of ecosystem services introduced in Section 2, and therefore with past species loss. The strong sustainability hypothesis implies that preserving ecosystems is especially important in regions or countries where physical capital is abundant, since nature becomes the limiting scarce factor. Our analysis nests both the case of economic activity that affects all ecosystem functions (which implies that conservation depends primarily on the most critical functions, even though other ecosystems are still relatively intact) and the case of multi-dimensional economic activity (such as more targeted land use) that opens the door for trade-offs between ecosystem functions and biodiversity offsets.

4 Biodiversity and the Economy: Evidence from Asset Prices

Our model suggests that biodiversity loss can negatively affect economic activity and make economies less resilient to future declines of biodiversity, such as those that will result from climate change. In this section, we provide empirical evidence for some of the mechanisms suggested by the model.

4.1 Empirical Approach and Testable Model Implications

Several factors complicate an empirical analysis of the relationship between biodiversity loss and the economy. First, changes in biodiversity are slow moving and economic output is only observed at relatively low frequencies, which makes identifying a causal relationship between these aggregate quantities challenging. In addition, as highlighted by our model, an absence of a relationship between biodiversity loss and current output does not mean that there are no meaningful economic effects, since some of the most problematic effects come through reductions in resilience to future shocks.

We therefore take an alternative approach to study the relationship between biodiversity loss and economic activity, 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 a stream of future cash flows, and should therefore also respond to changes in economic resilience that have not yet translated into changes in output. Second, while underlying economic activity and biodiversity loss move slowly, *news* about current and future biodiversity loss and resulting economic losses arrives more frequently, and asset prices will reflect such news immediately (as long as market participants view the news relevant for the stream of cash flows they are trying to price). As a result, researchers have more empirical variation to detect possible relationships.

Our model relates biodiversity loss to aggregate economic output for a given economy. We therefore look at CDS spreads, which capture the cost of insurance against default on government debt and, hence, reflect a country's aggregate economic outlook and expectations of aggregate economic tail-risk probabilities (Galil et al., 2014). Conceptually, bad news about biodiversity loss will lead to rising CDS spreads if market participants believe that such biodiversity loss will have meaningful consequences for countries' economic prospects that lead to higher default probabilities as a result. As such, CDS spreads can capture news about lower expected output as well as decreased resilience to shocks.

Our model predicts that news about biodiversity losses should affect economic output less if biodiversity is less degraded (see Proposition 1) or if biodiversity services are less binding for the production of economic output because other inputs are the constraining factor in production (see discussion of Figure 6). Empirically, we therefore estimate the extent to which these two factors mediate the effects of news about biodiversity loss on CDS spreads across countries, allowing us to test more nuanced implications of our model in the data. In addition, estimating such differential responses requires less stringent identifying assumptions than estimating the direct effect of news about biodiversity on CDS spread across the board. In the time series, biodiversity news might coincide with other news relevant to asset prices, which could confound our interpretation of the direct effect of news on asset prices. Estimating a differential response allows absorbing any direct effects on all asset prices, while still identifying differential effects in the cross-section.

4.2 Data

CDS Spreads. We analyze weekly changes in CDS spreads between 2001 and 2022. We use pricing information from Markit and include all CDS on government issued bonds with pricing data available. To abstract from changes in interest rate, we focus on USD denominated CDS.[32] We include maturities ranging from 1 to 30 years. Our sample includes CDS for government debt of 99 unique countries.

Negative Biodiversity News. To measure news about biodiversity loss, we build on the empirical work by Giglio et al. (2023), who produce an index of news coverage of biodiversity loss in the New York Times; to isolate the unanticipated component of news, we consider AR(1) residuals of the index, similar to the approach in Engle et al. (2020) and Alekseev et al. (2022). A higher score of $BiodiversityNews_t$, which is available at a weekly frequency, suggests the arrival of bad news about biodiversity loss.

State of Biodiversity. To measure the current state of biodiversity and how well preserved it is in a given country, we work with information from the 2022 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 a variety of environmental aspects. We focus on a subset of indicators related to biodiversity and ecosystem vitality (see Appendix A for details). Our main measure, $EPIBiodiversity + Ecosystem$ includes the two indicators from the EPI's biodiversity and habitat category which measure the physical state of nature (rather than regulatory measures): the change in biological diversity that has occurred in a country and the amount of suitable habitat remaining for each species. In addition, we include the EPI's indicators on changes in ecosystem services (tree cover loss, grassland loss and wetland loss) and fisheries. The EPI is available as of 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" (Wolf et al., 2022). In our baseline empirical analysis we average across measures at both points in time.

In robustness checks, we use several alternative measures. First, we focus only on the EPI indicators from the biodiversity and habitat category, excluding those related to ecosystem services and fisheries. Second, we also use the Environmental Vulnerability Index (EVI) which combines 50 indicators on a variety of aspects to gauge country's vulnerability to environmental hazards, including biodiversity loss. Finally, we use only the 2022 version of our baseline measure rather than averaging across the 2022 and earlier indicators.

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 renewable natural capital in a country's overall wealth. This measure is based on the World Bank's wealth accounting data and available from the ND-GAIN database, which provides a variety of indicators related to countries' adaptation to climate change.

Summary Statistics. Table 1 shows summary statistics of our final regression sample. Our data includes USD denominated CDS on government debt issued by 99 different countries. We include maturities, or tenors, ranging from 1 to 30 years. To ensure our results are not driven by outliers, we winsorize

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[32] In unreported results, including non-USD denominated CDS yields very similar results.

the weekly percentage changes in CDS spreads by 1% at the top and bottom. We analyze percentage changes in CDS spreads between 2001 and 2022, resulting in a sample of 443,175 weekly CDS spread changes across all maturities and issuers. The average weekly percentage change in CDS spread (after winsorizing) is 44 basis points, but there is a wide range: at the 10th percentile, CDS spreads have fallen by 7.7 percent and at the 90th percentile they have increased by 8.6 percent per week. Maturity or tenor ranges from 1 year to 30 years, with 5 year tenor being the most common at 18.7% of the sample and long maturities of 30 years being the least common at 15% of the sample.

Table 1: Summary Statistics

	Mean	**Standard deviation**	**p10**	**p50**	**p90**
Regression Sample (N=443,175)					
% Change in CDS spread (weekly)	0.44	9.07	-7.68	0.00	8.56
Tenor					
1 year (as % of sample)	17.73				
5 year (as % of sample)	18.73				
10 year (as % of sample)	18.05				
15 year (as % of sample)	15.09				
20 year (as % of sample)	15.44				
30 year (as % of sample)	14.97				
Biodiversity News (standardized)	0.04	1.05	-1.10	-0.10	1.36
EPI Biodiversity + Ecosystem (standardized)	-0.10	0.96	-0.94	-0.36	1.11
Natural Capital Share of Wealth (standardized)	-0.22	0.78	-0.90	-0.48	0.92
Biodiversity - Country Level (N=99)					
EPI Biodiversity + Ecosystem	32.24	11.26	22.33	28.94	47.37
EPI Biodiversity + Ecosystem 2022	31.05	12.99	19.28	27.60	46.79
EPI Biodiversity + Ecosystem (standardized)	0.00	1.00	-0.88	-0.29	1.34
Natural Capital Share - Country Level (N=89)					
Natural Capital Share of Wealth	0.13	0.13	0.02	0.08	0.35
Natural Capital Share of Wealth (standardized)	0.00	1.00	-0.90	-0.35	1.78

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 4 and section A. "% 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). "EPI Biodiversity 2022" is based on the EPI's biodiversity and habitat category and 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. "EPI Biodiversity + Ecosystem" adds indicators on ecosystem services (loss in tree cover, grassland and wetlands) and fisheries. Both indicators are available in 2022 and as a baseline measure around 2012.

The surprise component of biodiversity news is standardized to mean 0 and standard deviation of 1 over time. However, our panel is not balanced, and there are more observations in some weeks than others, leading the observation weighted average and standard deviation to differ slightly.

Similarly, we standardize the EPI Biodiversity and Ecosystem Score and the Natural Capital Share of Wealth 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.

Focusing at the country level, the non-standardized scores based on the EPI cover a (potential) range between 0 and 100. Our baseline measure averages over the versions for 2022 and those a decade earlier, but we also construct our measure using just the data for 2022. Both are vary similar with an average score around 31 and 32%. Across countries, the share of renewable natural capital is on average 13% of a country's wealth. But there is substantial variation with renewable natural capital only constituting 2% of wealth at the 10th percentile but 35% at the 90th percentile.

Appendix Tables A.1 and A.2 show our EPI based baseline measure and the share of natural capital for all countries in our sample. Focusing on the EPI Biodiversity and Ecosystem Score first, there is substantial variation within and across regions. Worldwide, some of the highest scores are observed in the Middle East. Countries with the lowest scores span a wide geographic range with Portugal, Uruguay, Malaysia and Ghana ranking at the bottom. These scores reflect that our measure assesses the state of biodiversity relative to the natural environment in a given country, rather than comparing biodiversity richness across different habitats. As such, our empirical measure aligns well with the metric of biodiversity loss used in the model, $s_g = S_g/\bar{S}_g$ as introduced in section 1.2.1, which also captures biodiversity loss relative to the initial maximum number of species present. Empirically, the high scores of many middle eastern countries reflect that large swath of their desert landscapes are still relatively un-eroded and endemic species are in comparatively good shape even though they tend to have lower species density than other habitats such as rainforests which boasts some of the highest density of unique species. However, there is also substantial local variation between countries with similar natural habitats. For instance, Jordan ranks number 4 worldwide, while neighboring Lebanon ranks 69th. Similarly, Cote d'Ivoire has the highest score within Africa, ranking number 12 worldwide, while neighboring Ghana has the lowest of all African countries in our sample ranking 96th worldwide.

Appendix Table A.2 shows the share of renewable natural capital in a country's total wealth. We use this metric as a proxy for how binding ecosystem services are for a country's economic output. A high share of renewable natural capital can stem from particularly high renewable natural capital or a scarcity of other capital. In both cases, a high share of renewable natural capital suggests that ecosystem services are unlikely to be the constraining factor of production. The distribution of this share across countries reflects both of these factors. Ethiopia has the highest share of renewable natural capital in our sample. This reflects both a relatively well-preserved state of biodiversity in the country (Ethiopia ranks number 20 out of 99 on the EPI scores) and relatively low levels of physical capital due to its low level of economic development, with Ethiopia's GDP per capita being one of the lowest in our sample. Conversely, some of the lowest shares of renewable natural capital are observed in the world's wealthiest countries. Singapore, one of the world's richest countries in terms of GDP per capita, has the lowest share of natural capital in our sample despite having comparatively intact nature as indicated by its 9th rank on the $EPIBiodiversity + Ecosystem$ score.

4.3 Empirical Analysis

Specification. We want to estimate the effect of negative news about biodiversity loss on CDS spreads and whether this sensitivity varies with country characteristics, namely the current state of biodiversity and the share of natural capital of a country's total wealth. To do so, we estimate the following equation: :

$$\begin{aligned}\%\Delta CDS\_Spread_{i,m,t} = \alpha &+ \beta_1 BiodiversityNews_t \\ &+ \beta_2 BiodiversityNews_t * State\_of\_Biodiversity_i \\ &+ \beta_3 BiodiversityNews_t * NaturalCapitalShare_i + \phi_{m,t} + \xi_{i,m,year} + \epsilon_{i,m,t}\end{aligned} \tag{29}$$

where $\Delta CDS\_Spread_{i,m,t}$ is the percentage change in the spread for CDS on country i, at maturity m, in week t. As described above, we focus on CDS denominated in USD and winsorize $\Delta CDS\_Spread_{i,m,t}$ at 1% at the top and bottom to make sure our results are not driven by outliers. $BiodiversityNews_t$ are unanticipated component about news about future losses from biodiversity loss as described above. A higher value constitutes more bad news. $State\_of\_Biodiversity_i$ and $NaturalCapitalShare_i$ are measured as described above. Both are standardized to have mean 0 and a standard deviation of 1 across countries in our sample to facilitate comparisons across regressors. We include two sets of fixed effects. First, we include maturity × time fixed effects, $\phi_{m,t}$, which capture other economic news such as changes in interest rates that could affect all CDS of a given maturity. When estimating the direct effect of $BiodiversityNews_t$, we include yearly fixed effects. We also estimate a version with CDS maturity × week fixed effects. This absorbs any time series variation in biodiversity news and thus subsumes any common effects of biodiversity news on all CDS spreads. But it allows us to estimate the interaction effects with less stringent identification assumptions. Second, we include year-specific fixed effects for each country × CDS type, $\xi_{i,m,year}$. These capture issuer- and type-specific effects that do not vary from week to week within the year. We cluster standard errors at the date × issuer level to account for the fact that all CDS for a given country might be affected by common factors.

Results. Table 2 presents estimates of equation (29). We pool over all maturities for each issuing country. In the first three columns we include year-by-tenor fixed effects to allow us to identify the direct effect of biodiversity news. The subsequent columns include week-by-tenor fixed effects, which absorb variation in biodiversity news but capture any additional factors that may affect CDS spreads in a given week, while still allowing us to estimate cross-sectional variation how negative biodiversity news affects asset prices. CDS spreads generally rise when bad news about future losses from biodiversity emerge. Specifically, a one standard deviation increase in adverse biodiversity news is associated with an average increase in CDS spreads of 16 to 17 to basis points.

Interacting biodiversity news with our two cross-country measures—the state of biodiversity and the natural capital share of wealth—allows us to analyze whether the sensitivity of CDS spreads to news about biodiversity systematically differs based on these two factors. The estimated coefficient on the interaction of biodiversity news and the country's current state of biodiversity is consistently negative, suggesting that CDS spreads are less sensitive to negative news about biodiversity loss for countries with healthier levels of biodiversity as predicted by Proposition 1. Magnitude wise, a one standard deviation improvement in the state of biodiversity in a country reduces the impact of a one standard deviation increase in negative biodiversity news by between 6.8 and 7.9 basis points. This is a 15% to 17% percent decrease relative to the average weekly change in CDS spreads of about 44 basis points.

Likewise, the estimated coefficient on the interaction of biodiversity news and a country's natural capital share of wealth is consistently negative. A higher share of natural capital suggests that natural capital is less likely to be a constraining factor in a country's production of output and, thus, the country's overall economy would be less susceptible to the effects of biodiversity loss. Our estimates indicate that a one standard deviation higher share of natural capital is linked to a 6.2 to 7.7 basis point reduction in the sensitivity of CDS spreads to biodiversity news. This amounts to 12% to 13% relative to the average weekly change in CDS spreads of 44 basis points. Overall, the estimated coefficients on the interactions remain similar regardless of whether only one or both interactions are included. Similarly, the estimates are unaffected by whether we simultaneously estimate the direct effect of negative biodiversity news or absorb this effect by tenor-specific date fixed effects.

Table 2: CDS Spreads Reaction to Biodiversity News

	% Change in CDS Spread (weekly)					
Biodiversity News	0.175***	0.171***	0.157***		omitted	
	(0.025)	(0.027)	(0.026)			
Biodiversity News * State of Biodiversity Score	-0.070***		-0.079***	-0.068***		-0.076***
	(0.022)		(0.025)	(0.020)		(0.023)
Biodiversity News * Natural Capital Share of Wealth		-0.067**	-0.077**		-0.062**	-0.072**
		(0.030)	(0.030)		(0.028)	(0.028)
Year * Tenor	x	x	x			
Week * Tenor				x	x	x
Country * Tenor * Year	x	x	x	x	x	x
N	443,175	403,047	403,047	443,175	403,047	403,047
N excluding singleton observations	443,111	402,993	402,993	443,095	402,977	402,977
Unique countries	99	89	89	99	89	89
Sample period	2001-2022					

Note: The table shows estimates of equation (29). The dependent variable is the weekly percent change in CDS spreads between 2001 and 2022, winsorized 1% at top and bottom. The sample pools across all tenors of USD denominated CDS for countries in our sample. $BiodiversityNews$ are measured by 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) with a higher number indicating worse news. $StateofBiodiversityScore$ is based on the Environmental Protection Index and contains a subset of indicators related to biodiversity and ecosystem services as described in the text; higher scores indicating less degradation of biodiversity. $NaturalCapitalShareofWealth$ is the share of renewable natural capital of a country's total wealth. All explanatory variables are standardized with mean 0 and standard deviation of 1 for countries in our sample. Standard errors are clustered at the date × issuer level. *(p<0.10), **(p<0.05), ***(p<0.01).

Interpretation. Our empirical estimates demonstrate that when negative news about future biodiversity losses emerge CDS spreads rise. This suggests that financial markets consider biodiversity loss as a material factor affecting countries' future economic output.

Furthermore, our estimates confirm two more specific predictions from the model. First, CDS spreads are less sensitive to biodiversity news in countries with less degraded biodiversity. This aligns with Proposition 1 which suggests that output is less affected by biodiversity losses at higher levels of remaining biodiversity. Second, CDS spreads are also less responsive to biodiversity news in countries with a higher share of renewable natural capital in their overall wealth. In such countries, ecosystem services are less likely to be the constraining factor of production, so biodiversity loss and the resulting loss in ecosystem services provided affect output less.

Robustness. In Appendix section A, we re-estimate equation (29) focusing only on CDS with tenor of 5 years—the most liquid tenor in our sample. The results shown in Table A.4 are very similar.

In Appendix Table A.5 we use our three alternative measures for the state of biodiversity. As outlined above, our first alternative measure excludes the ecosystem services and fishers categories of the EPI from our baseline measure. The second alternative measure is the Environmental Vulnerability Index (EVI) which captures a country's vulnerability to environmental hazards. Finally, we use only the 2022 version of the EPI, rather than an average across years as in our baseline measure. The results are very similar irrespective of the measure used.

5 Conclusion

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

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, 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. Policymakers should be aware of these non-linearities and proactively address threats to biodiversity before their economic impacts fully materialize.

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

Third, while biodiversity loss in developing countries may not substantially reduce economic output today given the abundance of ecosystem services relative to physical capital, it still imposes substantial economic costs by reducing future growth opportunities. Policymakers should therefore consider the intertemporal trade-offs associated with biodiversity loss, even if the near-term economic impacts appear modest. For example, in situations when current decision-makers do not fully internalize these long-term costs, implementing broad-based Pigouvian taxes on activities that destroy biodiversity could help protect the welfare of future generations.

Finally, the ecosystem fragility measures developed in the paper can help policymakers construct more complete assessments of the risks to the economy and financial system from nature loss. Quantifying these risks requires identifying which ecosystem services are most vulnerable to projected species losses, which the model shows depends on both the current depletion of biodiversity across different ecosystem functions and the degree of asymmetry in those losses. While more work is needed to empirically estimate some of the key quantities that determine the economic impacts of biodiversity loss, this paper provides a valuable framework to guide those efforts and a foundation for economists and ecologists to collaborate on addressing one of society's most pressing challenges.

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A Empirical Analysis - Further Details

In this Appendix, we provide further details on the empirical analysis presented in Section 4 of the main paper and 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

Environmental Protection 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 4, 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. 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, making interpretation of such a measure more difficult. The two indicators included in our first measure are the "Species Habitat Index" and the "Biodiversity Habitat Index". The "Species Habitat Index" (SHI) 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."* (see page 111 of EPI 2022 report Wolf et al., 2022). The "Biodiversity Habitat Index" (BHI) captures the *"change in biological diversity within a country due to habitat loss, degradation, and fragmentation across that country"* (see page 102 of EPI 2022 report Wolf et al., 2022). In addition to these two indicators, our measure also includes the indicators in the "Ecosystem Services" and "Fisheries" category. "Ecosystem Services" encompases three indicators: Tree cover loss, which measures *"the percent reduction in a country's tree cover in forested areas ... from the reference year 2000"* and grassland and wetland loss which are defined analogously but measured relative to 1992 as the reference year (see page 122 of EPI 2022 report Wolf et al., 2022). "Fisheries" includes three indicators: "Fish Stock Status" measures *"the percentage of a country's total catch that comes from overexploited or collapsed fish stocks"*. "Marine Trophic Index" (MTI) captures the *"ecological presssures on fish stocks"* by analyzing which trophic level or food web levels a country's fishing industry is targeting and "Fish Caught by Trawling and Dredging" measures the share of fish caught by these techniques with are particularly harmful to marine ecosystems (see page 114 of EPI 2022 report Wolf et al., 2022). The indicators compromising the EPI are available as of 2022, but there are also baseline versions of the indicators *"derived from applying the same methodology to data from approximately 10 years prior to current measurements"* (see page 24 of EPI 2022 report Wolf et al., 2022). In our main empirical analysis we average over the measures at both times. In robustness checks, we show our results are similar when using only the most recent measures from 2022. Tables A.1 shows our EPI based measure of biodiversity for each country in our sample by continent. Scores can range between 0 and 100 and a higher score indicates that biodiversity in a given country is less degraded. The rank of each country within our sample is shown in parentheses.

Table A.1: EPI Biodiversity + Ecosystem Score By Country

	EPI Biodiversity + Ecosystem				
	Score	**Global Rank**		**Score**	**Global Rank**
Africa	**30.9**		Switzerland	39.7	(17)
Côte d'Ivoire	44.7	(12)	Slovenia	38.1	(19)
Egypt	42.4	(15)	Finland	34.6	(26)
Ethiopia	37.7	(20)	Estonia	34.4	(27)
Angola	34.4	(28)	Bulgaria	33.8	(29)
Algeria	32.3	(35)	Latvia	32.9	(32)
Zambia	32.2	(36)	Croatia	32.1	(37)
Tunisia	31.5	(40)	Montenegro	32.0	(38)
Morocco	31.1	(41)	Austria	31.9	(39)
Rwanda	27.5	(60)	Slovakia	29.9	(44)
Cameroon	27.0	(65)	Hungary	29.2	(48)
South Africa	25.4	(74)	Sweden	28.9	(51)
Nigeria	23.6	(85)	Czechia	28.5	(52)
Kenya	23.5	(87)	Germany	28.5	(53)
Ghana	19.5	(96)	North Macedonia	28.5	(54)
Asia	**39.0**		Greece	27.6	(58)
United Arab Emirates	70.3	(1)	Italy	27.2	(63)
Saudi Arabia	69.0	(2)	Belarus	26.6	(66)
Bahrain	66.8	(3)	Russia	26.6	(67)
Jordan	65.6	(4)	Ukraine	26.5	(68)
Iraq	58.6	(6)	Lithuania	26.3	(70)
Azerbaijan	53.2	(7)	France	25.5	(73)
Singapore	48.5	(9)	United Kingdom	25.0	(76)
Oman	44.9	(11)	Ireland	24.1	(83)
Kazakhstan	44.7	(13)	Netherlands	24.1	(84)
Pakistan	43.8	(14)	Poland	23.5	(86)
Israel	38.2	(18)	Denmark	22.5	(89)
Georgia	37.6	(21)	Belgium	22.2	(91)
Qatar	37.6	(22)	Spain	20.7	(94)
Sri Lanka	35.6	(24)	Portugal	16.3	(99)
India	33.2	(31)	**North America**	**26.8**	
Philippines	32.6	(33)	Dominican Republic	32.4	(34)
Taiwan	31.0	(42)	Belize	30.6	(43)
Japan	29.3	(47)	Mexico	29.8	(45)
China	28.2	(56)	Barbados	29.5	(46)
Cyprus	27.1	(64)	Canada	28.2	(57)
Lebanon	26.4	(69)	Jamaica	27.6	(59)
Korea	25.1	(75)	El Salvador	25.6	(72)
Turkey	24.3	(80)	Trinidad and Tobago	24.8	(77)
Viet Nam	24.2	(81)	Panama	24.7	(78)
Thailand	21.7	(92)	Costa Rica	24.5	(79)
Indonesia	19.6	(95)	U.S.A.	22.8	(88)
Malaysia	16.8	(97)	Guatemala	21.2	(93)
Oceania	**27.7**		**South America**	**28.0**	
Fiji	33.3	(30)	Peru	37.4	(23)
Australia	25.8	(71)	Venezuela	34.7	(25)
New Zealand	24.2	(82)	Bolivia	28.9	(49)
Europe	**30.2**		Chile	28.9	(50)
Iceland	63.3	(5)	Ecuador	28.3	(55)
Malta	50.6	(8)	Colombia	27.4	(61)
Romania	47.4	(10)	Brazil	27.3	(62)
Norway	39.8	(16)	Argentina	22.3	(90)
			Uruguay	16.4	(98)

Note: The table shows the "EPI Biodiversity + Ecosystem" Score by country. Global rank within the sample is shown in parentheses. 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.

Environmental Vulnerability Index We use the Environmental Vulnerability Index (EVI) as an alternative measure for how degraded biodiversity is in a given country is. The EVI was devised by the South Pacific Applied Geoscience Commission (SOPAC) with the UN Environment Program and their partners and published in 2004 (Commission, 2005). It combines 50 indicators on a variety of measures to gauge the extent to which a country is vulnerable to environmental hazards. As such the EVI includes hazards from biodiversity loss, but does not exclusively focus on them. For the purpose of our empirical analysis, we re-cast the EVI such that higher values are associated with less vulnarability and standardize it to have mean 0 and a standard deviation of 1 in our sample.

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

We measure a country's share of natural capital by the share of renewable natural resources of a country's total wealth. We obtain this measure from the ND-GAIN 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 3 separate years: 1995, 2000 and 2005. For each country, we use the raw version of the indicator supplied by the ND-GAIN project and average over the years for which the measure is available. For the regression analysis, we standardize it to have mean 0 and a standard deviation of 1 across countries in our sample. Table A.2 shows the share of renewable natural capital for each country in our sample.

Correlation Table A.3 shows the correlation between the our different country level measures. The EPI Biodiversity and Ecosystem score is on average negatively correlated with the share of renewable natural capital with a correlation coefficient of minus 13%. This reflects that the two capture very different concepts. The EPI captures how well preserved biodiversity in a given country is relative to its original state. Hence, this measure is relative to a country's prior state but does not compare absolute values of biodiversity. The share of renewable natural capital, on the other hand, measures absolute values of renewable natural capital relative to a country's total wealth. Hence, it will be high if absolute values of renewable natural resources are high, irrespective of the extent of their degradation. As outlined in section 4 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 natural capital is lower for countries with substantial amounts of other capital irrespective of the state of biodiversity.

The lower part of the Table A.3 shows the correlation to alternative measures for a country's state of biodiversity. Our baseline measure, the EPI Biodiversity and Ecosystems, averages over information from 2022 and the same measures from a decade earlier. It is highly correlated at 95% with the version just using the 2022 information, suggesting that changes from a decade earlier are limited. Including

Table A.2: Share of Renewable Natural Capital By Country

	Natural Capital Share of Wealth				
	Share	Global Rank		Share	Global Rank
Africa	**0.249**		Latvia	0.098	(37)
Ethiopia	0.486	(1)	North Macedonia	0.086	(42)
Rwanda	0.471	(2)	Poland	0.075	(49)
Ghana	0.372	(6)	Lithuania	0.067	(51)
Kenya	0.365	(7)	Hungary	0.052	(57)
Nigeria	0.351	(9)	Slovakia	0.051	(58)
Zambia	0.295	(13)	Finland	0.051	(59)
Cameroon	0.271	(15)	Croatia	0.040	(61)
Côte d'Ivoire	0.245	(16)	Czechia	0.036	(63)
Angola	0.163	(25)	Ireland	0.031	(65)
Egypt	0.122	(34)	Sweden	0.031	(66)
South Africa	0.101	(36)	Greece	0.029	(67)
Morocco	0.086	(41)	Spain	0.023	(68)
Algeria	0.085	(44)	Norway	0.023	(69)
Tunisia	0.076	(48)	Denmark	0.021	(71)
			Iceland	0.020	(72)
Asia	**0.123**		Portugal	0.020	(73)
India	0.333	(10)	Austria	0.019	(74)
Pakistan	0.319	(12)	France	0.019	(75)
Viet Nam	0.293	(14)	Switzerland	0.018	(76)
Thailand	0.224	(18)	Italy	0.017	(78)
Indonesia	0.224	(19)	Netherlands	0.016	(79)
China	0.223	(20)	Malta	0.015	(80)
Azerbaijan	0.196	(21)	Germany	0.012	(83)
Philippines	0.178	(24)	Belgium	0.010	(84)
Sri Lanka	0.158	(26)	United Kingdom	0.008	(86)
Georgia	0.152	(28)			
Saudi Arabia	0.080	(46)	**North America**	**0.131**	
Turkey	0.067	(52)	Belize	0.394	(5)
Malaysia	0.064	(53)	Guatemala	0.324	(11)
Jordan	0.059	(54)	Costa Rica	0.146	(30)
Oman	0.039	(62)	Panama	0.131	(33)
Cyprus	0.034	(64)	El Salvador	0.089	(39)
Israel	0.015	(81)	Jamaica	0.088	(40)
Korea	0.015	(82)	Dominican Republic	0.085	(43)
United Arab Emirates	0.010	(85)	Canada	0.057	(55)
Japan	0.007	(87)	Mexico	0.043	(60)
Bahrain	0.005	(88)	Trinidad and Tobago	0.022	(70)
Singapore	0.000	(89)	U.S.A.	0.018	(77)
Oceania	**0.185**		**South America**	**0.172**	
Fiji	0.355	(8)	Bolivia	0.412	(3)
New Zealand	0.149	(29)	Ecuador	0.404	(4)
Australia	0.052	(56)	Brazil	0.153	(27)
			Colombia	0.141	(31)
Europe	**0.055**		Peru	0.102	(35)
Ukraine	0.243	(17)	Venezuela	0.094	(38)
Belarus	0.193	(22)	Chile	0.084	(45)
Russia	0.186	(23)	Argentina	0.079	(47)
Bulgaria	0.139	(32)	Uruguay	0.074	(50)

Note: The table shows the share of renewable natural capital of total wealth by country. Global rank within the sample is shown in parentheses. 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.3: Correlation between Country-Level Measures of Biodiversity and Share of Natural Capital

	(1)	(2)	(3)	(4)	(5)
(1) EPI Biodiversity + Ecosystem	1				
(2) Natural Capital Share of Wealth	-0.13	1			
(3) EPI Biodiversity + Ecosystem 2022	0.95	-0.18	1		
(4) EPI Biodiversity	0.45	-0.06	0.41	1	
(5) Environmental Vulnarability	0.05	0.30	0.02	0.43	1

Note: The table shows the correlation between our measures for the status of biodiversity and the share of natural capital. "EPI Biodiversity + Ecosystem" 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. The score averages over 2022 and the base year of 2012. "EPI Biodiversity + Ecosystem 2022" is based only on 2022. "EPI Biodiversity" 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. "Environmantal Vulnerability" is the Environmental Vulnerability Index (EVI) devised by the South Pacific Applied Geoscience Commission (SOPAC) with the UN Environment Program and their partners and published in 2004.

only the EPI indicators from the Biodiversity category and excluding those from the ecosystem category yields a correlation between the two types of measures of 45% (for the averaged version) and 41% (only 2022). This suggests that ecosystem services and fisheries capture different aspects of a country's natural resources. Finally, the Environmental Vulnerability Index is close to uncorrelated with our baseline measure. The correlation is higher at 43% when only biodiversity indicators of the EPI are included. Overall, the correlations suggests that our different measures for a country's state of biodiversity capture some common aspects but also each capture different aspects not captured by the others.

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

CDS Data. We obtain sovereign CDS data from Markit and include all CDS on sovereign debt contained in the database. We focus on the most liquid tenors (5, 10 and 1 years) as well as some less liquid tenors that span longer maturities (15, 20, and 30 years). We select CDS on the senior unsecured debt as it is more liquid, and keep the CDS with CR clause if available, otherwise MM, MR, and XR clauses (in this sequence); therefore, if available, we focus on CDS where the clause includes restructuring in the definition of the default event. We focus on CDS denominated in US dollars, and perform our analysis using the par spread (which is directly observed before the "big bang" of 2009 and is implied by Markit

Table A.4: CDS Spreads Reaction to Biodiversity News; 5 year, USD

	% Change in CDS Spread (weekly) - 5 year tenor, USD only					
Biodiversity News	0.151*** (0.024)	0.143*** (0.026)	0.134*** (0.026)		omitted	
Biodiversity News * State of Biodiversity Score	-0.046** (0.022)		-0.057** (0.024)	-0.051** (0.020)		-0.061*** (0.022)
Biodiversity News * Natural Capital Share of Wealth		-0.058* (0.030)	-0.065** (0.030)		-0.055** (0.028)	-0.062** (0.028)
Year * Tenor	x	x	x			
Week * Tenor				x	x	x
Country * Tenor * Year	x	x	x	x	x	x
N	83,000	75,496	75,496	83,000	75,496	75,496
N excluding singleton observations	82,994	75,491	75,491	82,994	75,491	75,491
Unique countries	99	89	89	99	89	89
Sample period	2001-2022					

Note: The table shows estimates of equation (29). The dependent variable is the weekly percent change in CDS spreads between 2001 and 2022, winsorized 1% at top and bottom. The sample includes USD denominated CDS with 5 year maturity for countries in our sample. $BiodiversityNews$ are measured by 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) with a higher number indicating worse news. $StateofBiodiversityScore$ is based on the Environmental Protection Index and contains a subset of indicators related to biodiversity and ecosystem services as described in the text; higher scores indicating less degradation of biodiversity. $NaturalCapitalShareofWealth$ is the share of renewable natural capital of a country's total wealth. All explanatory variables are standardized with mean 0 and standard deviation of 1 for countries in our sample. Standard errors are clustered at the date × issuer level. *(p<0.10), **(p<0.05), ***(p<0.01).

after it, so that we can concatenate the series across the two periods).

A.2 Robustness Tests

Table A.4 replicates Table 2 but focuses only on CDS of 5 year maturity, which is one of the most liquid and widely traded types of CDS. Results are very similar to the results pooling across all maturities. Consistent with this finding, unreported results show that estimates are also very similar when estimated separately for other maturities or when including CDS denominated in EUR.

Table A.5 explores robustness of our results to using alternative measures for a country's current state of biodiversity. The first column of Table A.5 replicates the last column of Table 2, whereas columns 2 to 4 use alternative measures. Specifically, in the second column of Table A.5, we exclude the ecosystem services category of EPI indicators from our baseline measure and instead only use the two indicators from the biodiversity and habitat category. The third column uses the Environmental Vulnerability Index (EVI). The last column measures a country's state of biodiversity using only the 2022 version of the Environmental Protection Index, rather than an average across years as in our baseline measure. The results are very similar irrespective of the measure used.

Our empirical analysis so far focuses on the percentage change in CDS spreads from week to week where we winsorize our the data at 1% at the top and bottom to ensure our results are not driven by outliers. We get similar results when winsorizing 5% at the top and bottom. Our results are also directionally similar when using absolute changes in CDS spreads instead of percentage changes, but the estimates are more noisy.

Table A.5: CDS Spreads Reaction to Biodiversity News; Different Biodiversity Measures

	% Change in CDS Spread (weekly)			
Biodiversity News	omitted			
Biodiversity News * State of Biodiversity Score	-0.076**	-0.057***	-0.072***	-0.073***
	(0.023)	(0.021)	(0.025)	(0.024)
Biodiversity News * Natural Capital Share of Wealth	-0.072**	-0.068**	-0.048*	-0.073**
	(0.028)	(0.028)	(0.028)	(0.028)
Biodiversity Score	Baseline	EPI excl. Ecosystem	EVI	EPI Biodiversity + Ecosystem 2022
Week * Tenor	x	x	x	x
Country * Tenor * Year	x	x	x	x
N	403,047	403,047	398,769	403,047
N excluding singleton observations	402,977	402,977	398,701	402,977
Unique countries	89	89	88	89
Sample period	2001-2022			

Note: The table shows estimates of equation (29). The dependent variable is the weekly percent change in CDS spreads between 2001 and 2022, winsorized 1% at top and bottom. The sample pools across all tenors of USD denominated CDS for countries in our sample. $BiodiversityNews$ are measured by 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) with a higher number indicating worse news. The measure of $StateofBiodiversityScore$ varies across columns. Column 1 uses our baseline measure based on the Environmental Protection Index, which contains a subset of indicators related to biodiversity and ecosystem services as described in the text. Column 2 excludes indicators in the ecosystem services category from our baseline measure. Column 3 uses the Environmental Vulnerabiltiy Indix (EVI). Column 4 uses only the 2022 version of our baseline measure rather than averaging across 2022 and 2012. For all measures, higher scores indicat less degradation of biodiversity. $NaturalCapitalShareofWealth$ is the share of renewable natural capital of a country's total wealth. All explanatory variables are standardized with mean 0 and standard deviation of 1 for countries in our sample. Standard errors are clustered at the date × issuer level. *(p<0.10), **(p<0.05), ***(p<0.01).

B Theoretical Appendix - Proofs

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

Proof of Proposition 1. Denote $Z_{-g} = E_{-g}^{\frac{\sigma-1}{\sigma}} = \sum_{j\neq g} a_j E_j^{\frac{\sigma-1}{\sigma}}$. We have

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

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

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 functions are complements, $\sigma < 1$, 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 $j \neq g$ fixed, it dominates the term in the bracket in (A.1):

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

hence

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

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. Define for any $\boldsymbol{s} = \left\{ s_g \right\}_{g=1}^{G}$ and $\boldsymbol{\theta} = \left\{ \theta_g \right\}_{g=1}^{G}$ the function

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

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

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

therefore

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

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

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

Defining

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

this rewrites

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

Turning to E,

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

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

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

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

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

and

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

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

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

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

and

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

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

Uniformly distributed idiosyncratic additive shocks. Decompose

$$ds_j = ds + dz_j$$

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

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

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

Then the expected effect is

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

With two functions $G = 2$ we have

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

thus

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

where

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

Proof of Proposition 5. The first-order optimality condition with respect to 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

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

The first-order optimality condition with respect to u is

$$\begin{aligned}
(1-u)\frac{L F_{L,0}}{Y_0 - K_1} &= \frac{\beta}{Y_1} F_{E,1} \frac{\partial E_1}{\partial \log(1-u)} \\
(1-u)\frac{Y_0}{Y_0 - K_1} &= \frac{\beta \eta_{E,1}}{\eta_{L,0}} \frac{\partial \log E_1}{\partial \log(1-u)} \\
1 - u &= \underbrace{\frac{Y_0 - K_1}{Y_0}}_{= \frac{1}{1+\beta\eta_{K,1}}} \frac{\beta \eta_{E,1}}{\eta_{L,0}} \frac{\partial \log E_1}{\partial \log(1-u)}
\end{aligned}$$

therefore

$$1 - u = \Lambda \frac{\partial \log E_1}{\partial \log(1-u)}$$

where

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

The comparative statics with respect to a_E, β, δ, $\boldsymbol{s}_0$ follow from the equation

$$1-u=\frac{\Lambda}{1-\Lambda\sum_{g=1}^{G}\phi_g\frac{\mu_g(\boldsymbol{s}_1)}{s_{g,1}}\frac{\partial\mathcal{L}}{\partial u}(s_{g,0},u)} \tag{A.3}$$

where as we note in the text that Λ is increasing in u. The left-hand side of (A.3) is decreasing in u while the right-hand side is increasing in u. The right-hand side is also increasing in β and a_E (through Λ). In the special case $\mathcal{L}(s_{g,0},u)=\delta u$ we have

$$\frac{\Lambda}{1-\Lambda\sum_{g=1}^{G}\phi_g\frac{\mu_g(\boldsymbol{s}_1)}{s_{g,1}}\frac{\partial\mathcal{L}}{\partial u}(s_{g,0},u)}=\frac{\Lambda}{1-\Lambda\delta\mathcal{F}(\boldsymbol{s}_0-\delta u\mathbf{1})}$$

which is decreasing in $\boldsymbol{s}_0$ (i.e., in each $s_{g,0}$) and increasing in δ.

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

$$\left[X_1^{\frac{1}{\xi}-1}+1+\beta\theta\right]X_1^{\frac{1}{\theta}}=\frac{\beta\theta\,(\bar{u}L)^{\frac{1-\theta}{\theta}}}{E_1(u)^{\frac{1}{\theta}}}F(K_0,uL,s_0) \tag{A.4}$$

$$1-u=\frac{\Lambda(u,X_1)}{1-\Lambda(u,X_1)\delta\mathcal{F}\left(\boldsymbol{s}_0-\delta u\mathbf{1}\right)} \tag{A.5}$$

where $X_1=\frac{K_1^{\theta}(\bar{u}L)^{1-\theta}}{E_1}$. The left-hand side of (A.4) 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.4) to get X_1 increasing in u and K_0.

Then the right-hand side of the second equation (A.5) 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 7. 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

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

but now

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

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

Therefore for each g

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

which can be rewritten as

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

hence summing over g

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