On the Economics of Extinction and Mass Extinctions

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Abstract

Human beings' domination of the planet has not been kind to many species worldwide. This is to be expected. Humans have radically altered natural landscapes, harvested heavily from the ocean, and altered the climate in an unprecedented way. Recent concerns over the extent and rate of biodiversity loss have led to renewed interest in extinction outcomes and speculation concerning humans' potential role in any future mass extinction. In this paper, we discuss the economic causes of extinction in two high-profile cases - Sharks and the North American Buffalo - and then extend our framework to allow for multiple species and the possibility of mass extinction. Throughout, we present evidence drawn from authoritative data sources with a focus on shark populations to ground our analysis. Despite large gaps in our data, the available evidence suggests extinction risks are rising for many species and policy is slow to react.

I Introduction

Humans (Homo Sapiens) are just one of over ten million species living on planet Earth - a statistic that belies our position as the world's apex predator and dominant inhabitant.[1] Over the past two millennia, our species rose from relative obscurity by altering natural landscapes for farming and then agglomerating industry in villages and towns. We spread ourselves across the globe by exploring new areas and exploiting new resources. Today, Homo Sapiens touch and transform every part of the earth.

What does this domination mean for millions of other species inhabiting the globe? Nature does abhor a vacuum: even the most inhospitable landscapes are fully populated and far from immune to our existence. Consequently, our expansion - the expansion of Homo Sapiens - has radically altered both the composition of natural populations and the number of existing species. We predate, for example, on almost a third of the world's vertebrates, with a range of prey perhaps 300 times greater than that of other, non-human, apex predators (Darimont et al. (2023)). The biomass of humans and our livestock alone is now more than ten times that of wild mammals and greater than that of all other terrestrial vertebrates combined (Bar-On, Phillips and Milo (2018)). And our influence on the climate and other natural systems is unprecedented (Rockström et al. (2009)).

At bottom, our expansion has been fueled by technological progress. Human ingenuity in harnessing everything from fire to nuclear fusion is the driving force behind our domination. And hence we ask how technological progress and its implications for growth and development, hasten extinctions.

One implication of technological progress is that it increases our ability to harvest from nature. It makes available new products and new methods to produce existing products at lower costs. Improvements in harvesting technology alone have provided some of the world's best-known extinction (or near extinction) events.[2]

A second implication of technological progress is the income growth it provides. Rising incomes raise consumption and may alter the composition of demand for unique status or luxury goods. Unfortunately, some of these goods are produced with natural inputs from small wild populations. A changing scale and composition of demand, tied to income growth,

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[1]There exists a debate among biologists on how to define a species. We follow the most widely accepted definition suggested by Mayr (1942) who defines a species as a group of natural populations that interbreed and reproduce in isolation from other groups.

[2]One prime example is the near extinction of the North American buffalo; see Taylor (2011) for a detailed account. Another would be the extinction of the passenger pigeon tied to the innovation of the telegraph which provided rapid information raising the productivity of hunting.

is a second cause of numerous past and ongoing extinctions.[3]

The third implication is that technological progress allowed humans to expand their spatial scale and geographic reach by reducing the costs of moving goods and people. Cheaper transportation means natural landscapes are now converted to farmland to sell highly prized crops in world markets; it means the inadvertent, but sometimes purposeful, introduction of destructive invasive species via ship ballast water, canal construction, and highways that fragment habitats; and finally, our use of fossil fuels to dominate the globe, has brought increased pollution and climate change that is currently, and in some locations rapidly, altering natural environments. Human expansions have produced numerous past extinctions, and climate change, in particular, may well bring an acceleration of future extinctions worldwide.Humans have long been suspects in many past extinctions, see Smith (1975) and Brander and Taylor (1998) for work by economists. See Cowie, Bouchet and Fontaine (2022) for an illuminating discussion of mass extinctions and humans' role in current biodiversity loss.

With this as a backdrop, we focus on two research questions. Why do extinctions occur? And is the rate of human-caused extinction likely to increase over time?

To help us organize our thoughts and data, we develop a simple general equilibrium model highlighting several key economy-environment interactions. It allows us to show how extinction is a natural process and all species are in some sense vulnerable. This vulnerability is, however magnified by human intervention and can lead to extinction outcomes increasing. The model is simple enough to identify the causal forces at work and just complicated enough to capture some unexpected general equilibrium and long-run impacts.

We use variants of the model to discuss two well-documented case studies of near extinction: the historic slaughter of the Plains Buffalo in the late 19th century United States and the ongoing slaughter of Sharks worldwide. These case studies provide clear evidence on the why of human-caused extinctions. Buffalo populations fell initially because of habitat loss but then dramatically because an innovation in tanning created a new market for raw buffalo hides. In the shark case, technological progress and new openness in Asia drove personal incomes higher and, with them, the demand for shark fin soup.

But case studies are, of course, just that. To answer our second question, we extend our model to allow for multiple species and use it to evaluate a wider set of evidence drawn from two authoritative data sources. We expand our discussion beyond case studies to provide an element of external validity. Our data sources paint a bleak picture of the future if current

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[3]An example is the decimation of sharks as discussed in Baum et al. (2003) and Erhardt and Weder (2020).

trends continue, but they differ greatly in their details. As its name suggests, the Living Planet Index created by the World Wildlife Fund (LPI) is very broad in its coverage and offers almost real-time measures of biodiversity changes worldwide. It is, however, a less credible guide to future extinction risks. In contrast, the Red List created by the International Union for Conservation of Nature (IUCN) offers detailed and credible population information but covers a small subset of the world's species whose assessments occur only periodically.

Both data sources contain thousands of species, so we sharpen our focus on their methods, comparability, and data reliability by investigating one well-documented class of species currently at risk - the Class Chondrichthyes (containing over 500 shark species). Using this as our test case, we find evidence of an ongoing serial depletion of shark species. This evidence is consistent across sources and suggests an important potential link between the initial decline of one population and the subsequent decline of another. In this sense, isolated case studies of individual species may provide only part of a broader picture of ecosystems under stress.[4]

To study this finding, we develop a multi-species extension of our model and show how this pattern of serial depletion can result when demand for the harvest good is transferred or concentrated on those species remaining. We call this assumption demand concentration and it can generate a series of boom and busts in harvests of individual species. The booms help maintain the aggregate, across-species harvest despite rapid population reductions for some others. This aggregation can mask an ongoing, very destructive process for the group as a whole.

Another way species extinctions can be correlated over time is if habitats are degraded by a common process such as climate change. This is, in essence, a supply side phenomenon. Habitat loss lowers populations' growth rate, making any species more vulnerable even without human harvesting. With habitat loss, multiple species can be driven to extinction, but earlier extinctions do not cause later ones. In contrast to demand concentration, slow and steady habitat loss produces slow and steady declines in individual and aggregate harvests as populations fall monotonically over time.

One interesting feature of both cases is that the order of species extinction is perfectly, but inversely, correlated with a population's growth rate. By itself, this result is not surprising. The compensatory nature of most natural growth functions economists work with ensures

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[4]There are many reasons why natural population sizes could be linked and correlated across time. In fisheries, serial depletion is often debated in the empirical literature started by Pauly et al. (1998) on fishing down (or through) the food chain (or web). For a theory of serial depletion where resources at the country level are depleted in sequence, see Copeland and Taylor (2006); see Eisenbarth (2022) for supporting empirical evidence.

that when populations decline, the percentage rate of growth of the species rises. This compensatory response works as a natural shock absorber: small populations grow faster and are, therefore, harder to drive to extinction. Our growth function exhibits this basic property (over a limited range). But when many species go extinct, we find that the natural ordering of extinctions - from slower to faster-growing species - also implies that the period between extinctions tends to lengthen. All else equal, it takes longer to drive a faster-growing population extinct. Consequently, it is very difficult for demand concentration or gradual habitat loss alone to generate a mass extinction event.

We generate a mass extinction by exploiting the complementarity between our two driving forces. Demand concentration raises harvests and pushes populations downward, which creates compensatory increases in this species' population growth. These higher growth rates would typically rule out extinction or lengthen the time to any extinction. However, when habitat loss is ongoing, it lowers any species' maximum percentage growth rate. This constrains the compensatory response, making the species under pressure more vulnerable. It tends to shorten the time to extinction. Putting these two forces together, we find that as habitat is degraded and demand concentrates, we generate what might be called a mass extinction: an extinction of multiple species that is compressed in time.

Since climate change *is* driving ongoing but slow habitat loss, does this mean that the rate of human-caused extinctions is likely to increase over time? It is unclear. If governments and international organizations are up to the task of documenting population sizes, identifying species at risk, and, if necessary, stopping population declines before they become extinctions, then there is no reason to believe the rate of human-caused extinctions will skyrocket in the near future. In fact, the rate of extinctions in many developed countries over the past half-century has fallen with the implementation of endangered species legislation of various forms. Unfortunately, this history of the developed world is probably less relevant than we think. Most of the world's remaining biodiversity lies in a relatively narrow band around the tropics, and countries in this zone are typically less developed, poor, and often have weak institutions. Linkages with major world markets are important for these countries, and international trade has the ability to concentrate world demand on relatively narrow products.[5]

This observation suggests that future species loss is an international problem that may need an international or transnational solution. The primary instrument for endangered species protection at this level is the Convention on International Trade in Endangered

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[5]Roughly three-quarters of the species on the CITES appendices are located in Africa, Asia, Central and South America, and the Caribbean; see https://speciesplus.net/.

Species of Wild Fauna and Flora (CITES). Accordingly, in the last section of this paper, we evaluate the success of CITES in protecting a large number of sharks in our test case of Chondrichthyes. We find evidence that both the LPI and the IUCN Red List warned of their endangerment long before any positive action was taken. Moreover, the actions eventually taken are only weakly protective and not inclusive of many threatened species. This suggests that absent changes, the rate of human-caused extinctions will rise and may rise rapidly. More is needed to protect species at risk, and we discuss some options in the penultimate section of this paper.

The rest of the paper proceeds as follows. Section II introduces the reader to the world's Big Five mass extinctions, provides a working definition, and discusses our two primary data sources. In Section III, we develop the model we used to guide our inferences and discuss the various paths to extinction. Following this we present two case studies of near and ongoing extinctions (Buffalo, Sharks) in sections IV and V. Section VI develops a multi-species model extension to examine some causes of multiple and mass extinctions. We close by using our data sources in Section VII to deepen our reasoning with data from sharks. We then ask whether protection for sharks has been forthcoming and briefly describe a path forward in Section VIII. A short conclusion follows in Section IX.

II Approaching the Sixth Mass Extinction?

A Mass Extinction is the extinction of a significant fraction of the world's species in a relatively short period of time. Time is measured against a geological clock and, therefore, "relatively short" is on the order of one to two million years. A *significant* fraction represents a number above 50%; a commonly cited benchmark is 75% of the world's species (Barnosky et al. (2011)).

Using this definition, the Earth has experienced five mass extinctions throughout its history. None of these extinctions was aided or abetted by human agency for the simple reason that they predate our earliest ancestors. Two of the mass extinctions were caused by asteroid strikes and their aftermath; one was caused by the violent geological activity of our young Planet Earth, but the remaining two resulted from relatively slow climate change. An informative graphic, adapted from the scientific literature, is shown below as a timeline.

Clearly, mass extinctions are very, very, rare events. Despite this, many scientists are drawing attention to the increased rate of extinction or near-extinction events caused by humans and asking whether we could be ushering in the first human caused - but sixth
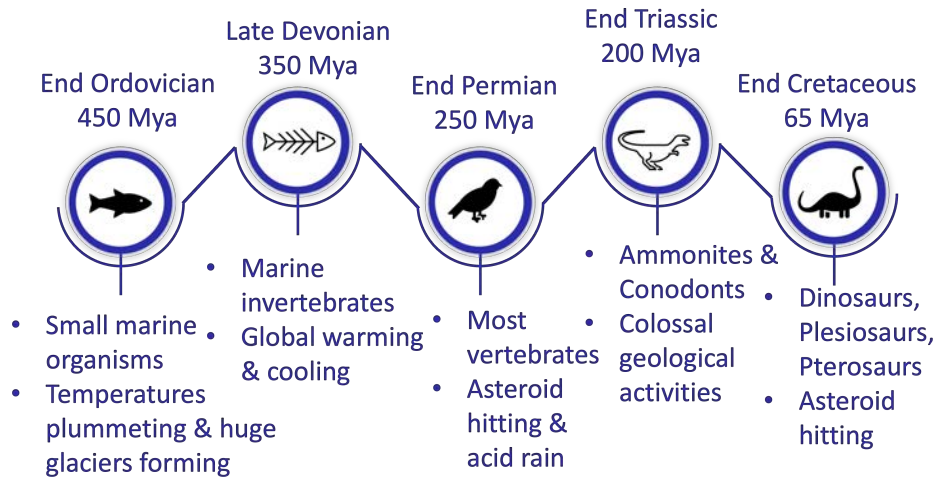
Figure 1: The Five Mass Extinctions. Source: based on Barnosky et al. (2011).

- mass extinction.[6] The prime suspects are habitat loss caused by either climate or land use changes, industrial pollution discharges, the introduction of invasive species, and human harvesting.

Any argument for an incipient mass extinction rests on three pillars: first, there must be a well-documented and significant acceleration in the extinction rate of various species; second, this increase in extinction rates must be a widespread phenomenon, affecting a broad range of species; and third, there should be compelling reasons to believe that these trends are not temporary but will persist or even intensify over time. There is robust evidence supporting the first criterion, moderate evidence for the second, and the third remains largely speculation.

To compare today's extinction rates to those in the past requires an estimate of the background, or baseline, rate of extinctions in the distant past. This background rate often comes from our incomplete fossil record.[7] Researchers then compare this background rate to a current rate of extinction constructed from data collected by the International Union

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[6]Barnosky et al. (2011) contains a very sobering introduction to the problems researchers face in identifying mass extinction events. For studies of specific groups see Wake and Vredenburg (2008), Ceballos et al. (2015), Ceballos, Ehrlich and Raven (2020), and Estes et al. (2011). For a very entertaining and enlightening account of extinction risks across the world, see Elizabeth Kolbert's excellent book "The Sixth Extinction: An Unnatural History", Henry Holt & Co. 2014.

[7]It is also possible to use molecular phylogeny to compare gene sequences, which allows us to understand evolutionary histories and hence extinctions. An earlier method used species-area relationships and knowledge about habitat loss to generate a benchmark, but this method has fallen out of favor.

for the Conservation of Nature (IUCN). In 1964, the IUCN established the "Red List of Threatened Species" which contains information on the extinction risk of animals, fungi and plants. In particular, it provides a continual assessment of a species' status regarding its risk of global extinction in the near future based on our current knowledge regarding population trends and perceived threats .[8] The more than 150,300 assessed species are categorized according to various levels of endangerment, ranging from "Least Concern" (LC: species that are widespread and abundant) to "Extinct" (EX: species that without any reasonable doubt lost the last individual).[9] In between these two extremes, species are divided into "Near Threatened" (NT), "Vulnerable" (VU), "Endangered" (EN), "Critically Endangered" (CR) and "Extinct in the Wild" (EW).

Using the IUCN data, researchers find current rates of extinction are far higher than those in the fossil record. For example, Ceballos et al. (2015) use data from the IUCN on extinctions since 1500 AD, and find, using only documented extinctions, that the extinction rate for vertebrates (animals with backbones) since 1500 - is eight times higher than the background rate. Moreover, extinction rates are also *increasing*. For example, using the shorter time period from 1900 onward they find the extinction rate for vertebrates is 22 times higher than the background rate. And these extinctions occur across all of the vertebrate classes. The figure below shows the widespread acceleration of extinction rates across different vertebrate classes. It shows the cumulative percentage of vertebrate species that became extinct (under a Conservative species definition) since 1500 AD. The figure depicts a large increase in extinctions since 1800 relative to the background rate shown by the dotted line.

To explain why the breadth and perhaps speed of extinctions will increase over time, authors need to assume little will be done to alter the current trajectories for climate change, habitat destruction, or human population growth. If these drivers remain in place, researchers predict that species currently at risk, or with small population sizes in the wild will go extinct in the next 100 years. Since many populations are on the brink of extinction with less than 1,000 members, the future rate of extinctions predicted by this method is very high.[10]

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[8]See the organization's homepage at //www.iucnredlist.org/.

[9]Some species are not in this classification because they are either "Not Evaluated" (NE) or "Data Deficient" (DD). See IUCN (2012).

[10]For example, Ceballos et al. (2015) create their Conservative aggregate (shown in Figure 2) by including not only those species truly extinct but also those "extinct in the wild" or "presumed extinct". While adding these two categories seems innocuous, their inclusion has a major impact on the results. Using the Conservative definition the rate of vertebrate extinction since 1900 becomes 53 times the background rate rather than just 22. Similarly, using another expanded definition Ceballos, Ehrlich and Raven (2020) find over 500 vertebrate populations are on the brink of extinction.
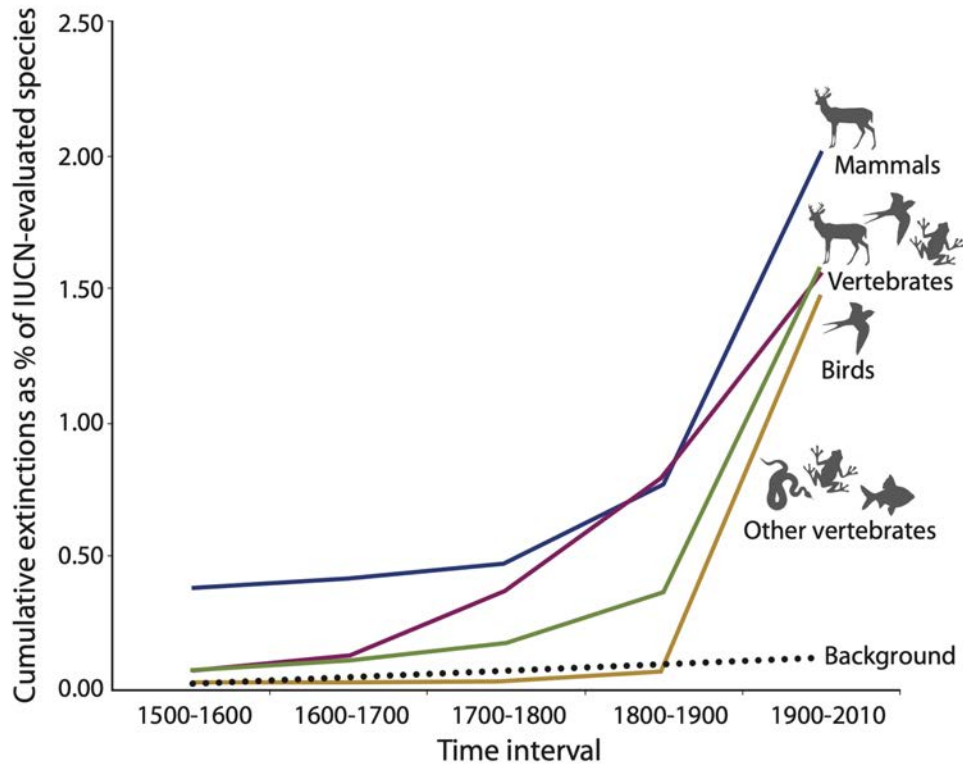
Figure 2: Conservative Count of Vertebrate Species Listed as Extinct, Extinct in the Wild and Possibly Extinct by IUCN (2012). Source: Ceballos et al. (2015).

An alternate method that also generates a bleak future is to base future predictions on past trends in biodiversity worldwide. The primary data source for this exercise is the Living Planet Index (LPI) developed by the World Wildlife Fund in 1997. The index uses data on the abundance of 5,268 species collected over 53 years from 1970 to 2022. It includes only vertebrate populations and therefore excludes not only all plants and fungi but also millions of other animal species.[11] The LPI comes in several different flavors: there is a global LPI, in addition to various sub-indices specific to either a given geography (North America, Asia, etc.) or the primary habitat of the species included (marine, terrestrial, freshwater). Two examples from the most recent WWF report are shown in Figure 3(a) and 3(b).[12]

Both of these indexes paint a bleak future for biodiversity worldwide. The global index, which is an aggregate across the different habitats globally, shows the index has fallen by

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[11]For example, Mammals that are in the Phylum Chordata (sub-phylum vertebrates) have approximately 4600 known species. Chelicerates are crab-like animals but not vertebrates; they have 75,000 known species, with 750,000 total estimated. Roundworms are also animals, but not vertebrates, and have perhaps 400,000 species; there are also many million species of insects and myriapods, etc.

[12]Figures 3(a) and 3(b) are from Almond et al. (2022), p. 32 and p. 36, respectively.

(a) The global LPI (1970 to 2018)
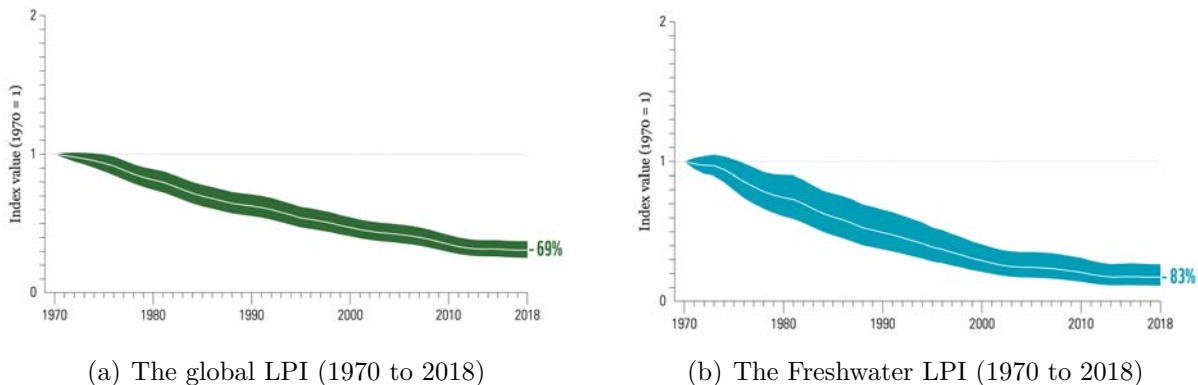

(b) The Freshwater LPI (1970 to 2018)

Figure 3: Living Planet Index
Source: Almond et al. (2022).

69% since its inception in 1970. A similarly horrifying number is shown for the Freshwater LPI. Since the shaded areas surrounding the trend estimates are bootstrapped 95% confidence intervals, the figures suggest the world has already experienced significant losses in biodiversity. It is tempting to conclude that any continuation of this trend could usher in a mass extinction.

III The Simple Economics of Extinction

To understand what might be driving extinctions, we construct a simple model relating human activities to the health of natural populations. Our economy produces two types of goods: M and H. M is the quantity of a typical (aggregate) manufactured good, while H reflects the quantity of a (aggregate) harvest good tied to nature. Consumers are identical and spend the fraction β on the harvest good H, and $(1 - \beta)$ on manufactured good (M).

The production of the harvest good depends on the health of a resource or natural population, which we denote by S and labor. Manufacturing requires only conventional inputs - labor. L denotes the total labor force and is fixed over time. φ captures scalar improvements in productivity economy-wide by raising labor productivity to φL. S reflects the health of the underlying resource and is proportional to the biomass (or population) of the species under consideration. The time path for S is determined by the scale of harvesting relative to natural population growth given by $G(S)$.

At a point in time, S is fixed, and the economy operates just like a simple two-good Ricardian model. The labor productivity in the two sectors equals $1/a_{LM}$ and $1/a_{LH}$, re-

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spectively. Consequently, if L_M and L_H are the allocations of labor across the two industries and production is CRS, outputs must equal $M = (1/a_{LM})\varphi L_M$ and $H = (1/a_{LH})\varphi L_H$.[13]

The level of harvesting affects the resource stock over time. In turn harvesting productivity is reliant on the health of the resource. To make this link explicit, we assume $1/a_{LH} = \alpha S$ and write the growth of the resource net of harvesting as $dS/dt = G(S) - H$. Since agents are atomistic, and their individual harvesting affects the health of tomorrow's resources, there is an underlying intertemporal externality. Actions today by anyone determine tomorrow's productivity for everyone.

We assume this market failure is not addressed. For clarity, we assume producers face no regulation in the harvesting sector. This implies the market structure is open access, and firms pay only the labor costs of their production. While open access might seem extreme, it can easily be the outcome if regulators have to monitor agents' take from nature. Copeland and Taylor (2009) employ a similar model but add a resource manager who limits how much an agent can harvest and fines those caught cheating. Since the manager faces a monitoring problem *de facto* open access is the equilibrium outcome for a set of economies they refer to as Hardin economies.[14] Open access is also the equilibrium outcome for all economies when resource prices are sufficiently low. Therefore, open access is less restrictive an assumption than might be thought.

III.I General Equilibrium Output

We can now determine the general equilibrium output of the harvest good for any given resource stock S. Given open access the supply price of the harvest good is $p_H = w/\alpha\varphi S$, national income is $I = wL$, and aggregate demand for the harvest good is $H = \beta I/p_H$. Using this information, we find the equilibrium harvest, for any S, is given by:

$$H(S) = \alpha\beta L S\varphi. \tag{1}$$

We refer to this as the harvest function. The intuition behind it is simple: a larger resource stock S or more productive harvesting technology, α, lowers the unit costs of production and via competition, lowers the price of the harvest good. This naturally raises the quantity demanded. Higher (φ) raises real income and demands uniformly, while a higher β signifies a

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[13]See Brander and Taylor (1997) for a detailed exposition of a very similar model.

[14]Hardin economies are those where the economy's productive ability is large (L, α, φ) relative to regulators enforcement power (high discount rates, short lifetimes, poor legal institutions).

stronger taste for the harvest good. At a point in time when S is fixed, the general equilibrium giving rise to the harvest function is shown in Figure 4 (we set $\varphi = 1$ to avoid clutter).
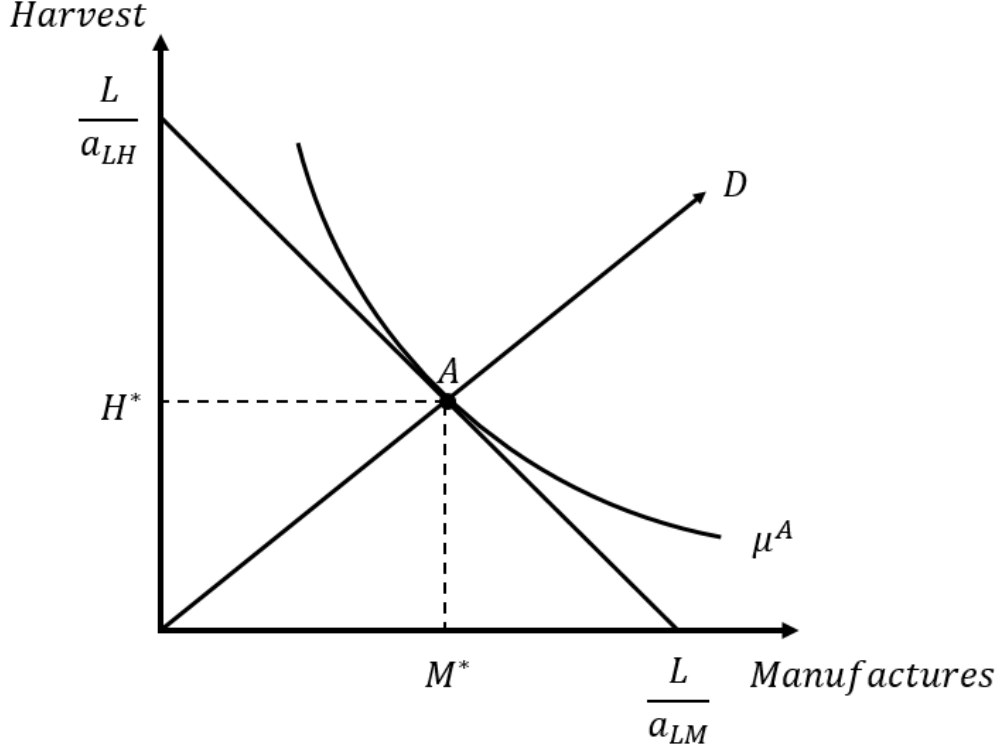

Figure 4: Equilibrium

While (1) represents the short-run take from the environment, over time, the population will evolve depending on a comparison of natural growth and our current demands. In order to determine the long-run equilibrium in the economy we have to account for natural growth $G(S)$. To do so we adopt an almost logistic specification that allows for extinction outcomes:

$$G(S) = rS(1 - S/K)(S/M - 1), \tag{2}$$

where K denotes the carrying capacity or maximum population size, $M > 0$ is the minimum viable population, and $r > 0$ is the intrinsic growth rate (note that $K > M > 0$). The key feature of (2) is that for small population sizes, $S < M$, population growth is negative. In Figure 5 we plot $G(S)$ and our harvest function $H(S)$ together.

For the moment focus on $G(S)$. Natural growth is negative for any stock below the minimum viable population M because G(S) is below the horizontal axis over this range. We might think of M as the population's point of no return: if natural disasters, predators or
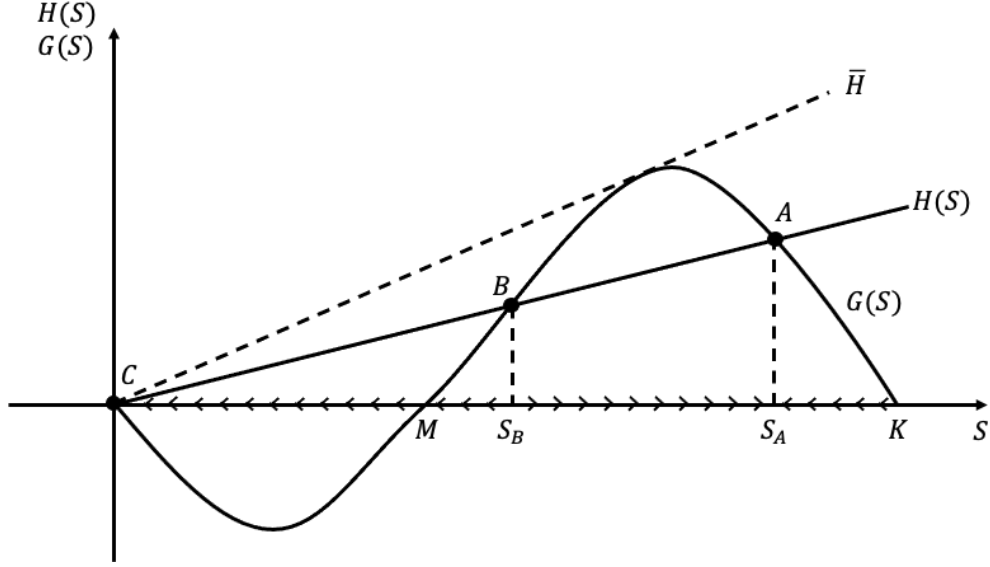
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Figure 5: Harvesting, Steady States and Extinction

invasive species lowered the population - even temporarily - below M, the resulting dynamics of the system drive the population to extinction.[15] Therefore, one possible long-run or steady-state outcome is extinction at $S = 0$.

Alternatively, any population above M would, in the absence of harvesting, grow until it reached the biological maximum at K. A population just equal to M is also a steady state, but any small perturbation drives the system to either extinction or toward its carrying capacity.

The growth function captures the idea that natural populations expand to fill their environment but are also inherently vulnerable to extinction. If M is very small or zero, the population is insulated from shocks; if M is quite large in relation to K, then even temporary shocks could easily tip the population onto an extinction path.

One way to make this idea of vulnerability more precise is to let:

$$v = M/K \qquad (3)$$

with $v \in (0, 1]$. If M is close to zero, then so too is vulnerability v; if M is close to K, then vulnerability is close to its maximum. By construction, v represents the fraction of

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[15]The biological rationale for a minimum viable population size comes from either the small probability of finding a mate in a very sparsely settled environment or reduced genetic variability in a small isolated population, lowering the probability of successful births.

all initial population levels below K, that generate extinction as the outcome absent human harvesting.

Now let's add the impact of humans represented by the harvest function $H(S)$. With active harvesting, the dynamics become slightly more complicated, and the likelihood of extinction rises. Growth is now determined by the difference between natural growth and human harvesting; that is, $dS/dt = G(S) - H(S)$ using (2) and (1). The intersection of the harvest and growth functions gives the steady states of the economy.

As shown there are three possible outcomes when humans are involved. First, the population could be zero with, therefore, zero harvesting and zero growth. Once at C, we remain forever. Second, at point B, harvesting equals natural growth, but any small positive or negative shock to the population generates further changes. A small positive shock moves us to the right of S_B where natural growth exceeds harvesting, which implies further growth amplifying the shock. The same argument is reversed for small negative shocks that move the population slightly below S_B. Therefore, the population of S_B, in a regime with active harvesting, plays the same role as did M when there was no harvesting. It divides the set of possible populations into those leading to extinction and those that do not. Notice that S_B/K, which is always greater than v, represents the fraction of all initial population sizes, given active harvesting, that lead to subsequent extinction. The simple observation is that any harvesting pressure raises the vulnerability of a species to extinction - an idea we will make precise in the next section.

Finally, point A represents the only interior steady state of the system where natural growth equals harvesting and is stable to small perturbations. Naturally, we focus our attention on steady states like A. But of course, the positive steady state at A only exists if the slope of the harvesting function - which is $\alpha\beta L\varphi$ - is not too large. "Too large" in the figure is identified by the slope of the hypothetical $\overline{H}$ function that is just tangent to $G(S)$. In other words, the larger the labor force (L), the larger the preference for the harvest good (β), the better the harvesting technology (α) or the more advanced is the state of the economy's technology (φ), the greater is the harvest function slope and the more likely the only stable steady state is at C.

But biology also matters. If the species in question reproduces faster, then it will, all else equal, be harder to drive this species to extinction. Less vulnerable populations will also be harder to drive to extinction. If we solve for the slope of the harvest function at $\overline{H}$ we find extinction will only occur if the demand side determinants - $\beta L\varphi$ - dominate those

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determining supply.[16] That is,

$$\beta L \varphi > \frac{r}{\alpha} \frac{(1-v)^2}{4v} \qquad (4)$$

The right-hand side of (4) falls if the species in question becomes more vulnerable, v rises, if its intrinsic growth rate is slower, r, or if it is easier to harvest, α. Therefore, for any given level of human demand, extinction is more likely if the population grows slower or is more vulnerable to extinction from natural shocks.

III.II   Paths to Extinction

Our simple model identifies four possible paths to an extinction outcome. One possibility is that shocks to birth or death processes push the population temporarily below M. These shocks could arise from newly abundant predators, weather variability, volcanic eruptions, scarce prey or disease. These shocks create what we might call *natural selection extinctions*. The rate of these extinctions per unit time, is what biologists refer to as the background extinction rate. The standard metric for this rate is extinctions per million species years. If 5 species of mammals go extinct over a period of 100 years, and if there were 10,000 mammalian species to start with, then the background extinction rate is 5 extinctions per million species years.[17]

To connect these background rates to our theory, start with a single population that has reached its carrying capacity with $S = K$. Assume this population is subject to negative shocks (for the reasons above), and in any given year, these shocks lower the population to some fraction of what it was before. That is, to γS for some positive fraction γ. Let these γ shocks be drawn from the continuous distribution function $F(\gamma)$. Then, the probability an individual population falls below M in a given year is simply the probability of drawing a sufficiently severe shock in that year. It requires drawing a $\gamma < \gamma_*$ where $\gamma_* = v$ is our measure of vulnerability. Any γ drawn below γ_*, drives the stock below M leading to extinction.

If these shocks are independent across time and species, and there are T years and I species, the expected number of extinctions is just the product $T \cdot I \cdot F(v)$. Therefore, in an uncertain world, populations will go extinct at rates determined by our vulnerability measure $v = M/K$ independent of any human intervention.[18]

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[16]See the Appendix for details.

[17]Because 100 x 10,000 is one million species years. See for example De Vos et al. (2015).

[18]This is why we have not adopted the typical logistic growth function where M is effectively zero. It is

A related path to extinction comes from the interaction of random shocks and human harvesting. In this case, we start with a situation where human harvesting has already lowered the population to the steady state at S_A shown in Figure 5. Since this population is lower than K, it is now easier for shocks to push the population towards extinction. Suppose we start with the population at S_A and nature generates a γ shock less than the new critical value of $\gamma_{**} = S_B/S_A$. The population immediately falls from S_A to below S_B, and absent immediate and compensating changes in demand, the population falls toward extinction. Notice human harvesting plays two roles here: it reduces the steady state stock closer to M; but it also changes the system's dynamics so that extinction arises whenever S falls below S_B and not the lower level of M. Both changes make extinction more likely.

The expected number of extinctions in TI species years is now given by $T \cdot I \cdot F(\gamma_{**})$ and this extinction rate is strictly greater than that without human harvesting $T \cdot I \cdot F(\gamma_*)$. It is worth noting that any change in fundamentals that shifts the harvest function in Figure 5 upwards lowers S_A and raises S_B. These changes increase the expected extinction rate because γ_{**} rises. Therefore, any amount of harvesting, even if it is sustainable under normal circumstances, raises the likelihood of extinction.

If we continue to shift the harvest function upwards (via changes in its determinants), it will eventually lead to a harvest function above $\overline{H}$ with C as the only steady state. In this third and direct path to extinction, the species has a commercial value, and harvesting continues despite a falling population and hence rising costs of capture. Harvesting could well cease before the population gets anywhere near zero; harvesting only needs to push the population below M. At that point, the species is a *dead man walking*; biologists use the less colorful term "extinction debt" to describe the set of future extinctions predetermined today.

Extinction arises here because we have pushed nature too far. To see this, notice that the slope of any ray from the origin through a point like S_A gives the percentage rate of species growth at S_A; that is, $G(S_A)/S_A$.[19] When there is little harvesting, S_A is close to K, and the species grows slowly; as harvesting pressure rises, the stock falls, and nature (initially) compensates with faster percentage growth, making extinction less likely. This compensation has a limit, however, and the maximal growth rate is reached when the harvest function

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inconsistent with a positive natural rate of extinction arising from random shocks.

[19]It is also the percentage growth at S_B.

becomes $\overline{H}$. At this point, the maximal percentage growth of our species is given by:

$$Max \{G(S)/S\} = r\frac{(1-v)^2}{4v}. \tag{5}$$

If we harvest from nature at a rate exceeding this maximum percentage growth rate, extinction has to result. Not surprisingly, this maximal rate is determined by the species underlying intrinsic growth rate r, but since our species has a minimum viable population, it also relies on our measure of vulnerability v, which brings us to our last path to extinction.

The last path to extinction comes from habitat loss. Changes in the climate alter habitats for natural species, forcing them to adapt at rapid rates. If habitat loss lowers K, it raises vulnerability, v. We have already shown that greater vulnerability raises the likelihood of extinction by natural shocks, raises extinction risks for species already harvested, and lowers the maximum harvesting pressure any one species can withstand (see (5)). Another more subtle form of habitat loss is fragmentation. Fragmentation is a case where K itself is untouched, but the habitat is effectively divided into two isolated segments with $K/2$. The purposeful clearing of forests for commercial farming and the introduction of roads can split or fragment habitats, creating genetic isolation.[20] Since the minimum viable population M remains the same in fragmented habitats, it's easy to see that vulnerability v rises making extinction more likely. Whenever habitat is lost or divided by human-driven economic activity extinction risks rise, and we can calculate those changes using our measure $T \cdot I \cdot F(v)$.

Extinction is a natural process driven by environmental variability and the pressures of natural selection, and therefore, some natural level of extinction is to be expected. But extinction also has human causes. Humans can be the primary driver when it arises from over-harvesting, or we can be a secondary driver when harvesting lowers populations, making them more susceptible to extinction via natural fluctuations. Moreover, humans may be responsible for habitat loss, raising populations' vulnerability. Consequently, we must ask whether there is good evidence of major extinctions driven by our behavior. And if so, will the rate of these human-caused extinctions rise over time?

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[20]Roads and other transportation infrastructure typically lead to the introduction of invasive species. For example, Egan (2017) contains numerous examples of how human interventions destroyed habitat on the Great Lakes. Some of these interventions were purposeful (introducing Coho salmon to Lake Michigan), and others were created by canal building (the sea lamprey and zebra mussel invasions).

IV The North American Buffalo (Bison)

Prior to European contact, the continental U.S. was home to some 25-30 million plains buffalo. They were found in all of the lower 48 states except New England, with especially dense concentrations in the productive grassland of the Great Plains (see Figure 6). Over the next two centuries, their numbers were steadily reduced by a combination of habitat destruction and subsistence hunting. The slow but steady movement of people westward removed all buffalo east of Wisconsin and in most of Minnesota by the 1830s. By the time of the California gold rush in the late 1840s, buffalo were gone everywhere east of the Mississippi, and by the end of the Civil War in 1865, there were only 10-15 million buffalo still wild on the Great Plains. But even here, their habitat was fragmented. It was divided in two by furious work efforts to complete the Union Pacific Railroad and the river of wagon trains carrying hundreds of thousands of pioneers traveling through the Platte River valley to reach California and Oregon. The buffalo retreated both north and south. The herds of buffalo in Montana, Wyoming, and the Dakotas became known as the Northern herd; buffalo in Kansas, Nebraska, Texas, Colorado, Oklahoma and New Mexico constituted the much larger Southern herd.

None of this history should be surprising: westward expansion meant farms and cattle ranches reduced buffalo habitat; towns, forts, railroads, and wagon trains fragmented it; and subsistence hunting to feed railroad crews, farmers, and townspeople meant the killing of buffalo for meat grew as Americans tamed their wild frontier. Despite these changes to buffalo habitat and numbers, observers at the time thought buffalo west of the Mississippi would decline at a pace much like the slow and steady destruction experienced by herds east of the Mississippi. No one foresaw that history would be far less kind.

Starting in 1871, and continuing over a span of a little more than ten years, the remaining 10-15 million plains buffalo were killed in a punctuated slaughter. The Great Plains were littered with rotting carcasses, stripped of their hide, but left otherwise untouched. Although most Americans are taught this *Slaughter on the Plains* was facilitated by railroads and perhaps perpetrated by the US Army, recent work in international trade has come to a very different conclusion. In Taylor (2011) one of us presented a case study where a combination of technological progress in tanning and free international trade in buffalo hides drove them very close to extinction. So close that a Smithsonian-funded expedition in 1888 led by (soon-to-be) famous naturalist William Temple Hornaday was sent to collect the last remaining buffalo from the scattered northern herd. From the tens of millions that once roamed the
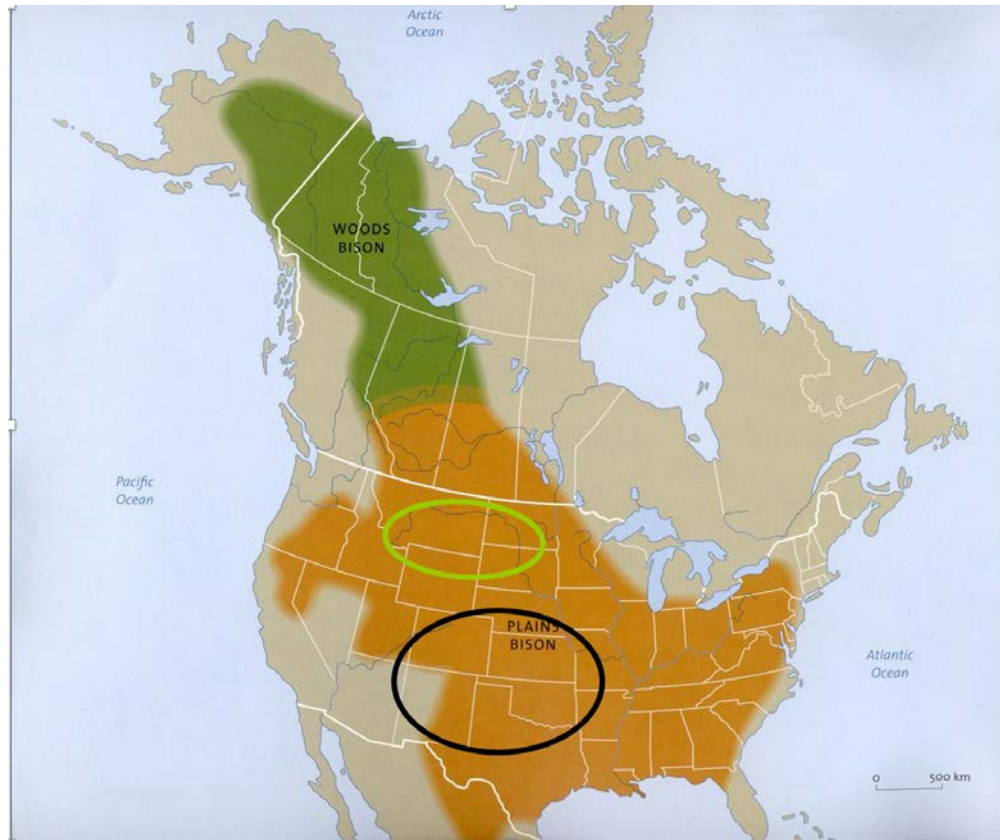
Figure 6: Pre-European Contact Range vs 1865 Northern and Southern herds
Source: Olson and Janelle (2005)

Great Plains, Hornaday found only perhaps 100 remained.[21]

IV.I The Innovation

The driving force behind the slaughter was technological progress. Two independent accounts tell almost exactly the same story. The first comes from a London Times dispatch from New York, reporting that in early 1871, a few enterprising New Yorkers' arranged for a bale of buffalo hides to be sent east to tanners in Pennsylvania and New York to see if they could be rendered into useful products.[22] Until that time, the market for buffalo products (meat and

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[21]Fortunately, other efforts at preservation were already underway in Texas by Charles Goodnight. See Taylor (2011) for further background on his efforts and their link to present-day herds in the U.S and Canada.

[22]"Buffalo Hides: Some eight or ten months ago," The Times, August 17, 1872, p. 4, Issue 27458, col. F. It is not known who the enterprising New Yorkers were, although one possibility is William C. Lobenstein (a pelt dealer with an office in Leavenworth, Kansas who "is well known as the first dealer to introduce buffalo hides to the market" (Fort Griffin Echo, April 19, 1879)).

buffalo robes) was constrained by both geography (robes could only be taken from herds in cold climates in cold weather months) and technology (railroad cars were not refrigerated). While this initial NY/PA experiment at tanning failed, several of the remaining bales made their way to England, where U.K. tanners soon succeeded in turning raw buffalo hides into useful, thick, and strong leather.

A second account comes from a direct participant in the slaughter. In an interview with former buffalo hunter George Hodoo Brown, he recounts his return to a meat hunting camp in May of 1871:[23]

As I came back in camp, I told the other fellers it was getting too warm to get the meat to market without spoiling. They says "Why don't you just skin them and let the meat lay", I says, "What the devil would I do with the hide", and they said ship it to W.C. Lobenstein in Leavenworth and he will send me a check. So next day, Burdett and I went a skinning.

These two accounts establish that, sometime in the spring of 1871, a new market was born. Brown's account is especially clear - hides were a worthless item before the innovation - but now buffalo everywhere and in every season had a price on their head. The value of a buffalo kill rose dramatically, and not surprisingly he and his partner Burdett went a skinning. The impact on the Great Plains was electrifying: meat hunters like Brown and Burdett became the first hide hunters while hundreds, if not thousands, of others soon followed in their footsteps. By 1872, a full-scale hide-hunting boom was underway.

Prior to hide-hunting the market for buffalo kills was determined only by domestic demand for meat or fur. Given the limits imposed on the meat market by transportation and the requirements of the fur market, the demand for buffalo kills was relatively small. In Figure 7 we associate this pre-boom purely domestic demand with the harvest function $H_A(S)$. As the population of the West expands the harvest function shifts upward raising this meat and fur demand to $H_{A'}(S)$. The buffalo herds diminish, but at a pace not too different from the slow but steady destruction witnessed east of the Mississippi.

In 1871 this all changed: once the easily transported buffalo hides could be sold at high prices, hunters flooded the field.[24] The relevant harvest functions jumped up to $H_T(S)$ where

[23]Interview with George W. Brown reported in Miles Gilbert, Leo Remiger, and Sharon Cunningham (2003, p. 55).

[24]The incentives were large. A typical four-man buffalo hunting crew had one hunter killing 60 buffalo/day; two skinners each skinning 30/day; and one camp cook keeping the accumulating hides and camp safe. In a 25-day month this crew produces 1500 hides with a market value of perhaps $3.00 each. Therefore, $4500 of total revenue is available to defray minimal costs before splitting it four ways with individuals having alternative employment earning $50/month on a ranch or railroad crew. In the early 1870s, buffalo hunting was a road to riches for anyone with a rifle and some ability to use it.
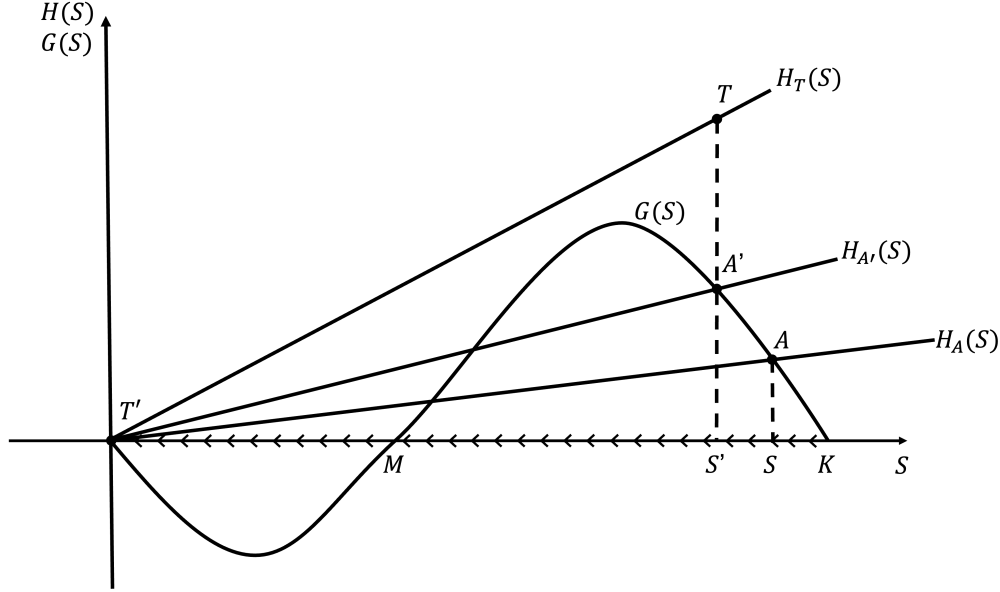
Figure 7: Slaughter

a much greater proportion of the labor force is now employed in hunting.[25] Anyone with a gun, a knife, and a wagon for transport can enter the new buffalo gold rush. As the slaughter proceeds, the herd naturally falls and we move towards the extinction outcome at T'. Hunters with limited skills leave as the buffalo become less numerous, but old hands like Hodoo Brown remain in the field because the price of hides is buoyed by a large world demand for industrial leather. By the year 1879, the buffalo are nearly extinct on the southern ranges and hunters must now move North. From 1881-1883 the Northern hunt plays out in a similar manner so that by the time Hornaday arrives with his expedition in Montana, he finds fewer than 100 buffalo remain wild on the Great Plains.

IV.II   The Evidence

While this is a wonderful story of extinction brimming with foreign intrigue and colorful characters, the logic rests on two unproven assertions. The first is simply that buffalo hide prices were unaffected by the slaughter which maintained the incentive to continue hunting despite falling numbers. In Table 1 below, we present market hide prices in the New York market over the 1866-1885 period.

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[25]Before 1871, demand is determined by the autarky harvest function in (1) and growth in L is shifting it up as shown. Once there is trade with relatively high hide prices, the frontier economy now specializes in hunting. The harvest function shifts up sharply since specialization is the equivalent of setting $\beta = 1$ in (1).

Year	WP	NY	HP	Year	WP	NY	HP
1866	4.56	4.74	0	1876	3.25	4.04	2.32
1867	4.12	4.82	0	1877	3.40	3.42	2.43
1868	3.93	4.43	0	1878	2.96	3.03	2.12
1869	4.18	4.66	0	1879	3.12	4.51	2.23
1870	3.99	4.51	0	1880	3.53	3.58	2.52
1871	3.93	4.35	2.81	1881	3.40	3.42	2.43
1872	4.06	4.35	2.90	1882	3.37	3.26	2.41
1873	4.12	4.35	2.94	1883	3.34	3.34	2.38
1874	3.99	4.20	2.85	1884	3.46	3.26	2.47
1875	3.84	3.89	2.74	1885	3.28	3.58	2.34

Notes: WP is hide prices found using the Warren and Pearson price index. NY is hide prices found using data drawn from the Annual Reports of the New York Chamber of Commerce. HP is the price-to-hunters series. Source: Table 1 in Taylor (2011).

Table 1: Hide Prices (Dollar/Hide)

The first two columns represent slightly different estimates for hide prices in NY; the last column is an estimate of the price obtained by hunters. Prices in the first two columns show that hide prices moved slightly lower over the entire period, but there is little evidence of a strong trend. The N.Y. price series, which is actual transaction prices, shows no trend at all over the 1871-1879 period and a flat trend over 1881-1883. This is not surprising because while the number of buffalo hides exported by the US was significant by US standards, they were very small relative to the world market for hides.

The second piece of important information comes from data on U.S hide exports. Taylor (2011) presents data obtained from U.S. exports of hides drawn from various years of the United States, Department of Treasury, Bureau of Statistics, Foreign Commerce and Navigation of the United States.[26] Since this data is often in value terms, it was first deflated by the price series shown to generate a series of hide exports in quantities. Since hides includes both cattle and buffalo hides, he employs a well-known model of the U.S. cattle industry to remove possible cattle hides from the export numbers. The result is the constructed buffalo hide export series shown in Figure 8.[27]

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[26]These are now available online through the Archive of Americana, US Congressional Serial Set, 1817–1980, published by Readex, a division of Newsbank, Inc. at http:// infoweb.newsbank.com/.

[27]An alternative quasi-experimental method using rawhide import data from European countries produces very similar results. See Taylor (2011) for details.
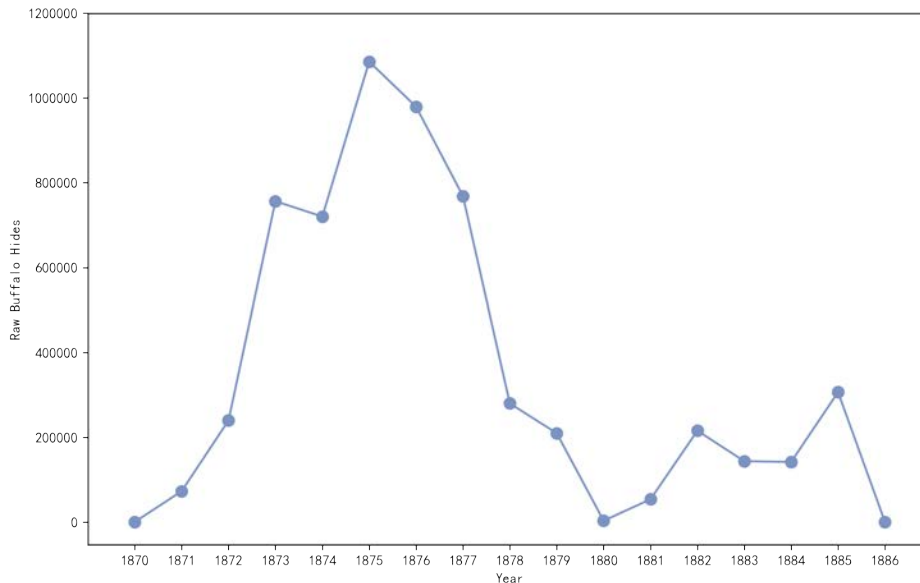
Figure 8: Buffalo Hide Exports During The Slaughter

The slaughter began in early 1871 in Kansas and Nebraska, but by the end of 1874, buffalo hunters needed to move south into Texas, Oklahoma, and New Mexico. An estimate by Colonel Richard Irving Dodge (then resident in Kansas) put the 1872-1874 hide shipments by rail at 1.4 million hides; the number from the export figures shown above puts it slightly higher at 1.7 million. When buffalo were gone from Kansas and Nebraska, the slaughter moved south. 1875/6 were the peak years for buffalo hunting, with the last buffalo hunts in Texas in 1879 destroying remnants of the Southern herd. In 1881, the hide hunters turned northward, and soon, the Northern herd was also destroyed.

In total, the export data shows over six million buffalo hides exported, but these figures ignore the many lost to wastage. Dodge, for example, reports large wastage in the early years, with every hide shipped in 1872 representing 3 buffalo killed. In 1873 this figure fell to 2, and then to 1.25 in later years. Applying these estimates, the export of 6 million represents a kill of closer to 9 million buffalo. Since a kill of 9 million does not exhaust the 10-15 million thought to be resident on the Great Plains, there is still ample room for wasteful hunting by settlers and wanton killing by the U.S. army. Nevertheless, the driving force behind the slaughter was a foreign-made innovation and a healthy foreign demand for industrial leather.

Ultimately, the buffalo did not become extinct, and some would say their domination of the Great Plains had to end anyway. And while elements of U.S. society were shocked and horrified by the slaughter, no legislation regulating their hunt was passed in time. Political

differences, bureaucratic delay, and a belief that fewer buffalo remaining would mean a more docile native population won the day, while the power of international markets ensured their very rapid destruction.

V   Sharks

Most of us are terrified of sharks. On television and in movies, they appear suddenly from dark water and with deadly effects. In reality, sharks are mostly shy and peaceful around humans. They have an astounding capability to use electromagnetic fields for hunting and have survived numerous glaciations, climate events, and even an asteroid strike but in the last few decades, they have fallen victim to the most dangerous hunter on earth - the human being. Today, more than 150 species of sharks are threatened by extinction, with some populations collapsing to less than 20% of their historical abundance.[28]

Our widespread fear of sharks - and resulting neglect of their majesty - is perhaps why the general public has long ignored the severe depletion of sharks. The cause of this depletion is easy to identify, and in Erhardt and Weder (2020), one of us argued that international trade in shark fins is the main driver of these changes.

V.I   International Trade of Shark Fins

Most shark hunting is driven by the demand for shark fins that, in turn, are mainly consumed in Asian countries in the form of shark-fin soup. There is a long tradition (particularly in China) of shark-fin-soup consumption at special occasions (weddings, New Year, banquets). Whereas shark-fin consumption was discouraged during the Mao area (1949-1976), it gained popularity under Deng Xiaoping (1979-1997) with a "relaxation of state market control, increased disposable income, and growing official acceptance of shark fin consumption" (Rose, 1996, p. 49). By the turn of the century, shark-fin soup had become a "day-to-day, integral component of Chinese culinary identity" consumed by much of the general public (Cheung and Chang, 2011, p. 355).

The final consumers of the shark-fin soup are largely indifferent as to which shark species' fin ends up in their soup. The processing of a shark fin (e.g., how the fibres or needles inside the fin are removed in the cooking process and prepared), the combination with other ingredients and the ambiance in a restaurant are much more important. Not surprisingly,

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[28]See, for example, Baum et al. (2003) and Clarke et al. (2013).

consumers of shark-fin soup are typically not informed about the name of the shark species that delivered its fin. The fishery industries collect sharks from all over the world, their fins being removed and sent to mainly Asian countries. The fins pay a high price on the shark-fin market and are thus the main driver of shark hunting. Partly influenced by some countries' ban on shark finning (i.e., the widely used practice to cut off the fins from still living sharks and throwing the shark bodies overboard), a market for shark meat has recently evolved with a relatively large demand outside Asia, particularly from Latin America (see Dent and Clarke (2015)). This market can, however, mainly be regarded as a byproduct of the market for shark fins.[29]

In Figure 9 we graph worldwide imports of shark fins from its first year of reporting, 1976, to 2021 with imports divided by major importing countries.[30] Three observations are in order. First, imports of shark fins have grown tremendously. From their relatively low and stagnant levels in the late 1970s and 1980s, to levels triple these in the 2000s. Second, the primary nation driving this burgeoning demand is China with Hong Kong as a processing and trading hub of shark fins, although in recent years other Asian economies—including the rest of Far East and South East Asia (RoFESEA)—have become important markets (and hubs). Approximately 90% of worldwide imports of shark fins (by weight) have traditionally been going to seven Asian economies: China (incl. Hong Kong), Singapore, Malaysia, Taiwan, Sri Lanka, Japan and Thailand. The first four economies have traditionally been the major shark-fin importing countries, with an average share of 80%. Apart from Asia, the rest of the world (RoW) imports a small but rising fraction of world supply. Finally, it's important to note that demand has remained high despite a changing composition of importers.[31] Therefore, import demand has not only tripled over the period, it remains very high today.

V.II Global Capture and Heterogeneity

Imports are not production or the capture of sharks, and hence in Figure 10, we present worldwide capture statistics that are available since 1950 (expressed in tonnes of the live weight of sharks). Worldwide production of all sharks, in yellow, mimics, to some extent,

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[29]Note that sharks are also victims of bycatch, being hooked or entangled in various fishing gears.

[30]FAO (2023a), "Global Aquatic Trade Statistics 1976-2021" (FishStatJ). Shark Fins include all forms (fresh, dried, smoked etc.); see the Data Appendix for more information on how we constructed the time series, particularly for China (including Hong Kong) to take into account re-exports of Hong Kong.

[31]The steady increase in the RoW is likely a consequence of the increase in the Chinese or, more generally, Asian diaspora in these countries. Note that the sharp increase in 2021 of the RoW is mostly due to a reported increase of Ukraine's imports of shark fins from 108 tonnes (2020) to a surprising 3626 tonnes (2021).
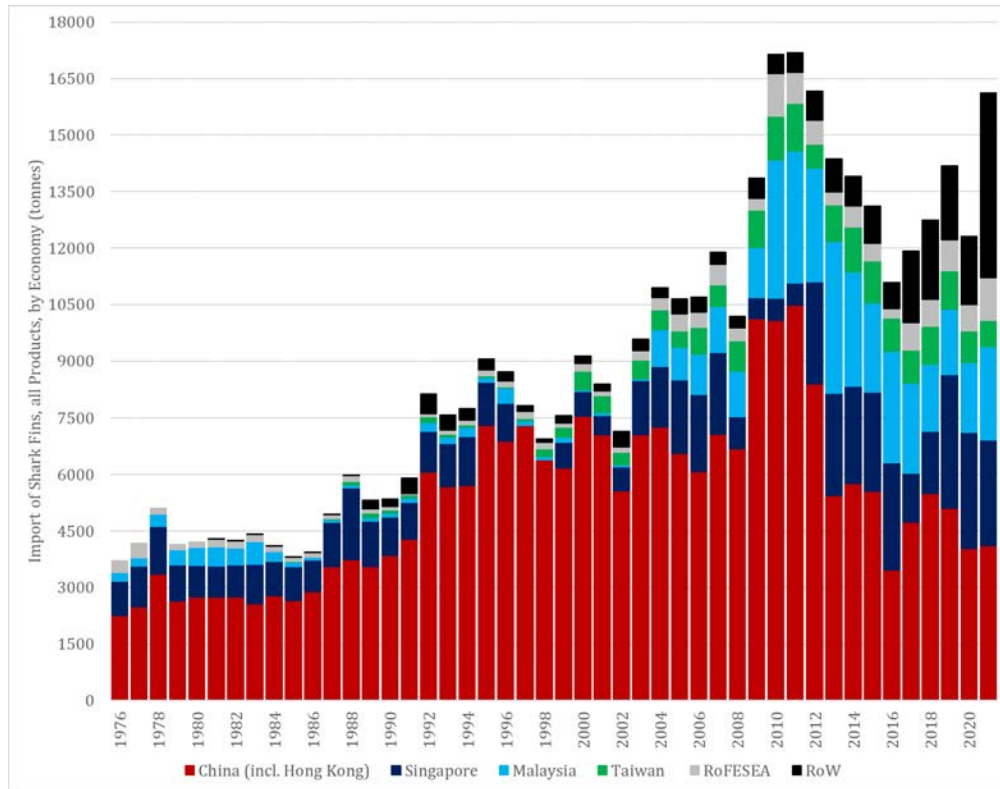
Figure 9: World-Wide Imports of Shark Fins (Weight of Fins)

that of imports of shark fins. It starts relatively low in the 1950s, steadily increasing thereafter to reach a plateau in the 1970s and 1980s; it then climbs in the early 1990s to peak in 2000 and then takes a decreasing trend. In addition, we can show that the global shark-fin trade is indeed the main driver of shark hunting as the implied shark biomass of the global shark-fin trade turns out to be at least as high as the world capture of sharks (1976-2000).[32]

The top five shark-hunting countries had together a share of 50% of the world capture of "All Sharks" (average of 2012 to 2021), led by Spain (14%), followed by India (10%), Indonesia (10%), Taiwan (8%) and Mexico (8%). The Pacific Ocean traditionally was the major fishing area for sharks, but considerably decreased in importance over the last decades, whereas the Atlantic and Indian Ocean became more important, with a minor role of the

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[32]Note that "All Sharks", "Requiem Sharks", "Hammerhead Sharks" and "Thresher Sharks" are groups of shark species; see the Data Appendix for the exact list of shark species which are included in these groups from FAO (2023*b*) "Global Fishery and Aquaculture Production Statistics 1950-2021" (FishStatJ). For the calculation of the biomass of shark-fin imports we use our data depicted in Figure 9, distinguish between dried and wet fins and apply the formula from Erhardt and Weder (2020), p. 4. We then compare the result with the world capture of "All Sharks" in Figure 10.

Mediterranean and Black Sea.[33]

Also shown in the figure are captures of individual shark species or groups of shark species for which long-time series exist. To highlight them individually, they are graphed on the right-hand axis (except for the Blue Shark). Interestingly, the production of the groups as well as the individual species of sharks, have a largely similar pattern of increased harvest, peak harvest, and then decline. The overall production figures are therefore buttressed by sharks entering and then largely exiting production.

Reading from left to right, the Porbeagle showed an early peak capture in 1964 (9,674 tonnes), quickly falling to a 1,000 tonnes thereafter and further diminishing to a production of approximately 100 tonnes or less since 2015. A similar example is the Basking Shark, which reached its peak production in 1970 (18,700 tonnes), then steadily declines to 389 tonnes in 2000 and further fell in the following years. Next, the Tope and Silky Shark enter production only to peak and then be replaced by the Thresher Sharks. The Blue shark, which is hunted in large numbers (and we therefore measure on the left-hand scale), began production relatively late before reaching its peak harvest in 2012 (167,639 tonnes) and then declining. Note that the Blue Shark has recently reached a relatively high share of 30% of world capture of all sharks.

Two sharks seem to belie this tendency. The Requiem Sharks start relatively early with a steady increase in production to a peak in 1996 (55,198 tonnes) only to fall off very late in the sample. Similarly, the Hammerhead Sharks production may still be rising. In both cases, however, these represent groups of sharks. Both are composed of a large number of related, but different shark species. As a group they have been hunted in large numbers over most of the sample period, and individual shark species within these aggregates largely show the same pattern of rising production, exhaustion, and falling harvests as shown by all other species.

An important feature of sharks that may explain this pattern of sequential exploitation is heterogeneity across sharks in their intrinsic growth rates. This may not come as a surprise, given their large differences in size (from less than a meter to more than 10 meters) or lifespan (from 5 to more than 100 years). The large sharks are apex predators that are particularly vulnerable to decimation because their survival strategies did not develop under situations with high mortality (see Clarke, Milner-Gulland and Bjørndal (2007)).

Worm et al. (2013) for example provides data on the growth rates of 62 shark species

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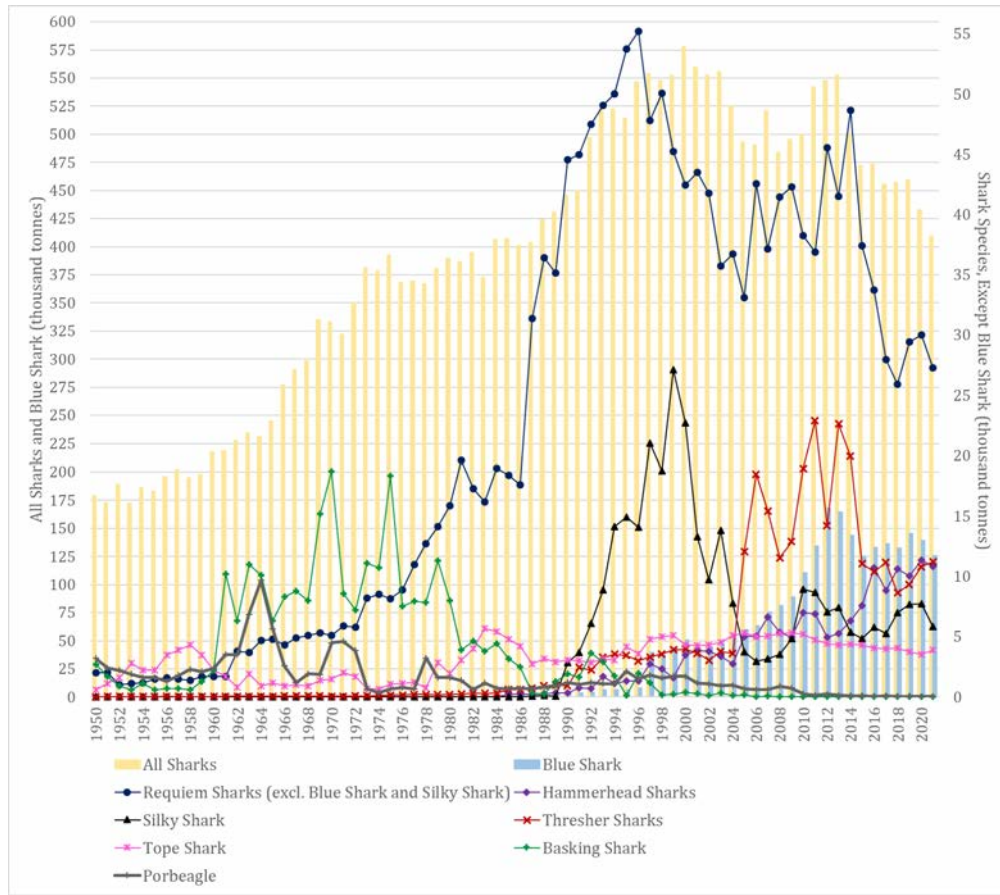[33]Own calculation based on FAO (2023*b*), using our definition of "All Sharks".

Figure 10: World Capture of Shark Species and Groups of Sharks (Live Weight of Sharks)

showing they differ by a factor of 13 between the slowest and fastest growing shark species.[34] The early peaking Porbeagle and Basking Shark are characterized by relatively low reproduction rates, while the later peaking Blue Shark has a higher rate. The Requiem Sharks, however, includes a large number of shark species with low, medium and high intrinsic growth rates.

We can understand these developments with the help of our model. In Figure 11 we depict two steady states at A and A' for two different species of sharks. Demand, represented by the harvest function, is the same for the two species shown because harvesting for shark fin soup does not discriminate across sources. Demand captured by H_A is currently quite low, representing conditions at the start of our sample. The growth functions for our two species

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[34]This is between the "Leafscale Gulper" with a rebound rate of 0.0095 and the "Grey Smooth-Hound" with a rate of 0.121. In our context, rebound rates are proportional to intrinsic growth rates. See Erhardt and Weder (2020) for more details.

differ because one species has a higher intrinsic growth rate, r, than the other. This implies $G(S) > G'(S)$ as shown (for $M < S < K$).
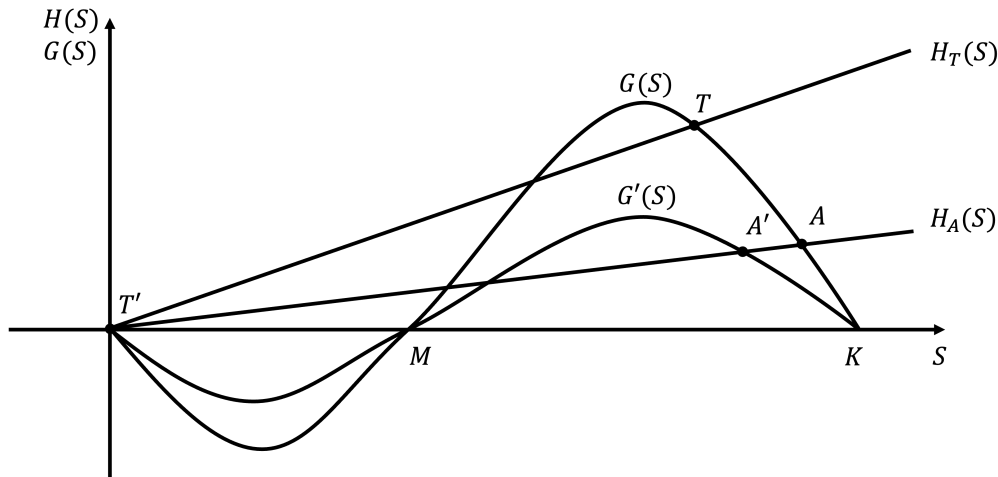

Figure 11: Shark Hunting

Over our time period, 1976-2018, there were three major changes. An increased demand for shark fins — as a major ingredient to the luxurious shark-fin soup - arising from cultural changes during the Deng Xiaoping era (raising β); a steadily rising population in Asia (L); and a very large increase in real incomes (φ) in Far East and South East Asian countries largely driven by liberalized trade and technological progress. Together these forces raised the value of a shark kill and the harvest function shifts upward to H_T.

The harvests from both species of shark start to rise. Harvests from the slower-growth species rise, peak, and then fall along the harvest function H_T. This slower-growing species is destined for extinction. Harvests from the faster-growth species rise and stay high at T. While both populations decline, overall production from all sharks would first rise and then fall, mimicking the patterns in Figure 10.[35]

VI   Extinction in a Many Species World

While the buffalo and shark cases are provocative case studies, how common are they? Are the Buffalo and Shark cases unique - or is the earth, or some portions of it, entering a new

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[35]Notice that demand from slow-growing species going extinct may be shifted on to its faster growing relative, creating a second increase in demand. The possibility of extinction concentrating demand and creating sequential extinctions is considered in the next section, including the possibility of habitat loss that increases the vulnerability of a species.

phase of rapid extinction as humans increasingly transform the global environment? These are incredibly difficult questions to answer.

To help us answer these questions, we now extend our model to many species. The hope is that a many-species model may provide new insights into the likelihood of extinction for many related species. The key modeling question we must answer is how do these many species interact. Species in the natural world are interconnected through a complex array of relationships: competitive, parasitic, and symbiotic.[36] These are what we might call supply-side (general equilibrium) connections. But similar difficulties lie on the demand side - how are the demands for harvests from these species connected? Adding either supply or demand side connections can easily render the model useless as a tool for understanding.

Consequently, we adopt three simplifying assumptions to maintain the model's tractability. First, we allow our many species to differ in only their rate of regeneration, r. Second, we assume the harvest consumed from these species are substitutes in demand. In some cases, we will allow demand to concentrate on those species remaining when a subset goes extinct. And lastly, we assume that any shock that degrades the carrying capacity for one species does so for all species. Degradation is a form of habitat loss, and we model it as an increase in v. Habitat loss can occur because of land conversion to agriculture, from the introduction of invasive species that out-compete native varieties, or from changes in the quality of habitats arising from climate change or increased economic activity.

VI.I   Many Species Model

Let z index species and label them so that $r(z)$ increases in z. Let our continuum of species z range over the interval $[0, 1]$, and assume $r(z)$ is continuous and differentiable. Other determinants, such as vulnerability v and the harvesting technology α, are common to all species. Using equation (4), we can then define the $SS(z)$ schedule as:

$$SS(z) = \frac{r(z)(1-v)^2}{\alpha 4v} > 0, \;\; with \; r'(z) > 0. \tag{6}$$

$SS(z)$ is an upward-sloping schedule reflecting the heterogeneity across species in their intrinsic growth rates. It is bounded both above and below because $\infty > r(1) > r(0) > 0$. If we graph $SS(z)$ against z, we find it shifts down if the set of species experiences habitat loss or

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[36]For example, we could model the species as predator and prey, host vs. parasite, as competing species; as symbiotic, or exhibiting either commensalism or amensalism. The possibilities are virtually endless. See Pielou et al. (1969) for an extremely lucid introduction to the issues.

fragmentation (K falls or is fragmented, which raises v); if their minimum viable population rises (M rises which raises v); or if their harvesting technology improves. A uniform increase in the set of intrinsic growth rates would shift the schedule up, as would habitat restoration or restrictions on harvesting technology. We think of $SS(z)$ as representing the potential (steady-state) "supply of extinctions" across our continuum of species.

To capture the demand side, we follow our simple model in assuming fixed and equal expenditure shares across all species. Let $b(z)$ be the expenditure share for species, z, then $b(z)$ integrated over $[0,1]$ equals β the overall share of expenditure spent on harvests. Equal budget shares across species imply the density of demand is some constant $b = b(z)$, and therefore $b = \beta$ of income falls evenly on all existing species. This implies the demand function for any species is $H(z) = \beta I / p(z)$.

In the very long run when a species goes extinct, the demand that would have fallen on a now-extinct species must be attributed elsewhere.[37] There are only two possibilities. One possibility is to allocate this demand to manufacturing, keeping the expenditure spent on the remaining species unchanged. By construction, the set of species going extinct will be some set $[0, \bar{z}]$, where $\bar{z}$ is the marginally extinct species. If we keep the demand facing all remaining species constant in the event of some extinctions, the overall share of income spent on harvests from those remaining becomes $\beta(1 - \bar{z})$ and the share of income spent on manufactures becomes $1 - \beta(1 - \bar{z})$. These shares imply the density of demand falling on the surviving species remains the same because $\beta(1 - \bar{z})/(1 - \bar{z}) = \beta$.[38] We take this as our base case and refer to it as the case of diffuse demand.

Another possibility is to shift the demand from extinct species to those species remaining. For example, if one shark species goes extinct, demand for those remaining could rise because they are very good substitutes in consumption. In this case, extinction concentrates demand. If the fraction of species going extinct is $\bar{z}$, then the density of demand for the remaining species shifts up. Their demand function becomes $H(z) = [\beta I]/[p(z)[1 - \bar{z}]]$ and this implies the fraction of income spent on harvests in total remains at β, but it is concentrated on those species remaining. We refer to this as the case of concentrated demand.[39]

In either case, we substitute into the demands $H(z)$, $I = wL$ and prices, $p(z) = w/[\alpha \varphi S(z)]$

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[37]See the Appendix for more details.

[38]For example, suppose 70 percent was originally spent on seven harvestable species and 30 percent on manufacturing. If one species goes extinct, $70(1 - 1/7) = 60$ percent of income is now spent on the remaining six harvestable species, and 40 percent of income is now spent on manufacturing.

[39]Following our previous example, the now remaining six species have 70 percent of demand falling on them, and their density of demand went from 10 percent pre-extinction to $70/6$ percent after extinction. Manufacturing has 30 percent of expenditure allocated to it throughout.

to find the species-specific harvest function. Combining the harvest and growth functions, much like we did in Figure 5, allows us to determine which species survive and which go extinct. Since $SS(z)$ captures the supply side determinants, we now construct a complementary $D(z)$ schedule that captures demand side parameters. To see how this apparatus works, we start with the simpler diffuse demand case and graph both schedules in Figure 12.

$SS(z)$ is shown as the upward-sloping function. $D(z)$ is the multi-species equivalent of the demand side determinants in equation (4), and under diffuse demand, it is independent of z and therefore given by the horizontal line: $D(z) = \beta\varphi L$. Their intersection at B identifies a borderline species determined implicitly by $SS(z_B) = D(z_B)$. For any species to the left of this borderline, for example, z_A, we have $D(z_A) > SS(z_A)$, which implies the extinction condition in (4) is met. These species are destined for extinction (absent some intervention). To the right of the borderline species, at, for example z_C, we have instead that $SS(z_C) > D(z_C)$ and the conditions for extinction are not met. A positive long-run population exists for all of these species.
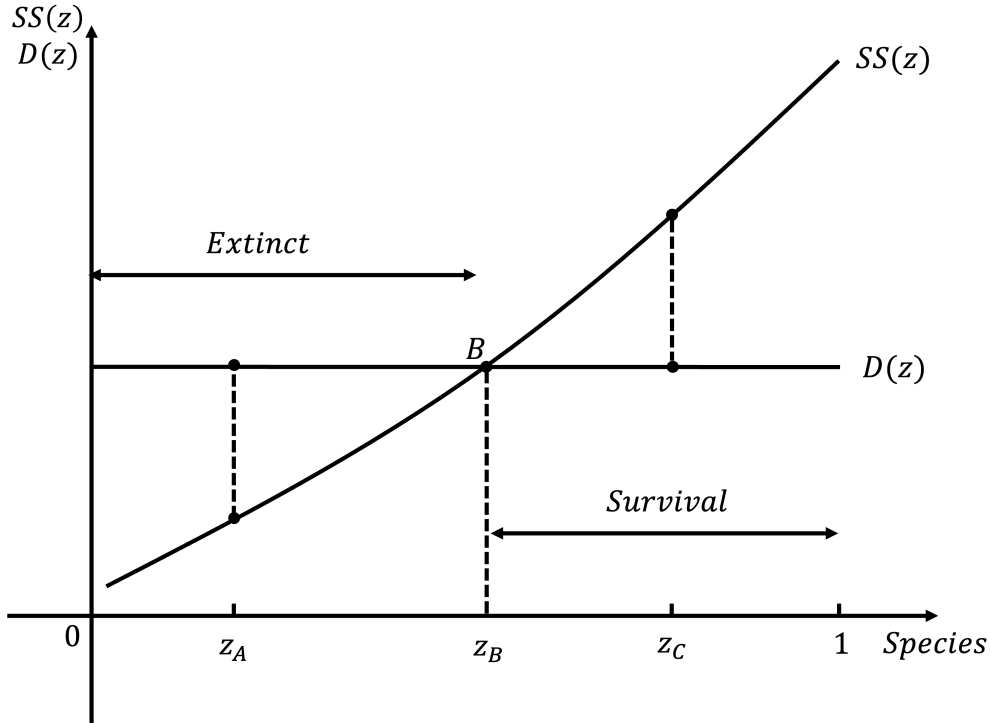

Figure 12: The Supply and Demand for Extinctions

The figure depicts only steady-state outcomes, but our data is unlikely to represent long-run snap-shots of steady states. The simplest solution is to simulate the model and trace

out its transition dynamics. To do so, we assume a finite number of species and endow them with different intrinsic growth rates. In Figure 13, we assume there are twelve populations initially at their carrying capacity (K) which we have normalized to one. The species differ in their intrinsic growth rates, and to distinguish across the species in our graphs, it proves useful to assume the physical quantity harvested of any species is inversely proportional to its intrinsic growth rate. This means a unit of harvest (e.g., an individual) from a fast-growing species represents fewer kg of harvest than does a unit of harvest from a slow-growing larger species.[40] As shown in the left panel, only two of the twelve species go extinct; ten others approach interior steady states. In this simulation M=.7, which implies that any surviving species must have a steady state population greater than $[K + M]/2 = .85$. Any species whose population falls below this value is destined for extinction, and their population falls precipitously soon after breaching this limit.[41]

In the right panel, the harvests follow the time series of their populations very well. In ten cases, these adjustments are small, but for the two species going extinct, harvests fall rapidly because the productivity of harvesting is proportional to the underlying population size which from the left panel is falling rapidly.

Clearly, a positive demand shock shifting $D(z)$ upwards would move our borderline species to the right in Figure 12, and our simulations would change accordingly. This could come about from the integration of new markets into the global economy; a shift in demand towards consuming the harvest good; or come from rising incomes tied to technological progress driving all demands upwards. More than two species would go extinct, and these would be the slowest growing of those remaining.

Similarly, a once-for-all supply shock could have similar effects. This could be because of an improved harvesting technology, the destruction of habitat, or just economic growth and agglomeration fragmenting natural landscapes with roads, fences, or pipelines. In all these cases, the steady-state supply of extinctions shifts down because either α or v rises. The new equilibrium would feature more extinctions, but the slow-growing species remain the most vulnerable.

Distinguishing between a demand and supply shock-driven extinction will be difficult. In some cases, it may be possible. For example, if all the species in question were resident domestically with stable supply conditions, then it may be possible to identify a foreign demand

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[40]This is just to make the figure more readable; nothing hinges on it. There is a negative correlation between body mass and growth rates across much of the animal kingdom.

[41]All parameter values are given in the Appendix.
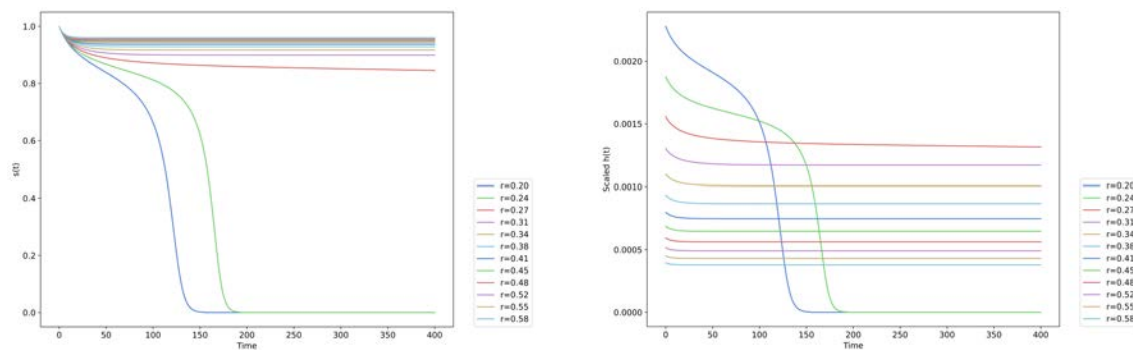
(a) Solution of the differential equation for different r values

(b) h(t) for different r values

Figure 13: Diffuse Demand & Habitat Intact

shock as the driver of a particular extinction. The shark case is primarily a demand shock extinction; in contrast, the buffalo case is primarily a supply shock (technological progress) extinction. But in many other cases, supply and demand determinants are clearly linked. The economic growth of cities and transportation networks drive income gains, demands, and in many cases fragments habitats. New markets brought about by international trade generate demand shocks but may also introduce invasive species raising vulnerabilities.[42] To a certain extent, these difficulties are why the case study evidence is so important.

VI.I.1   Concentrated Demand and Serial Depletion

We now consider the possibility that the extinction of some species concentrates demands on those remaining. We contrast two possible steady states in Figure 14. One steady state is at point A and follows from assuming diffuse demand. The other steady state is at B' and comes from concentrated demand.

The concentrated demand schedule $D(z)' = D(z)/[1-\bar{z}]$ lies everywhere above the diffuse demand schedule except at the vertical axis. For example, consider point A with a set of extinct species $[0, z_A]$. Under diffuse demand, the expenditure share spent on the extinct species shifts to manufacturing and the steady state in this case is at point A. Alternatively, if the demand for these extinct species is concentrated on those remaining, then the demand relevant for those remaining, when z_A are extinct, is much higher at A'. But of course, A'

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[42]See for example McAusland and Costello (2004) and Costello et al. (2007) for a discussion of invasive species and their damage to ecosystems. See Egan (2017) for a very engaging but absolutely frightening account of how invasive species (sea lampreys, alewives, zerbra and quagga mussels) were introduced into the Great Lakes because of canals constructed to facilitate international trade.
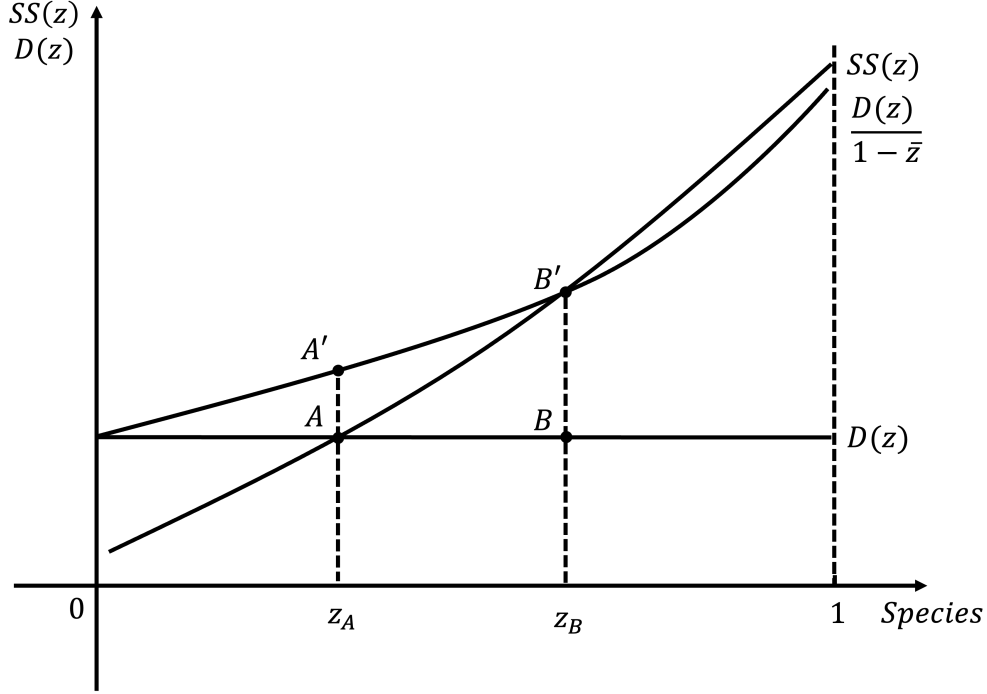
Figure 14: Concentrated versus Diffuse Demand

isn't a steady state, and the set of extinctions rises to z_B with the intersection at B'.[43]

To understand how the concentration of demand might affect what we could see in data, we present a simulation much like that presented earlier. This simulation differs in only one respect: we assume that when a species goes extinct its demand is reallocated to those remaining. Using exactly the same parameter values as in our earlier figures, we now find five of the twelve species go extinct as shown in figures 15(a) and 15(b).

Initially, the harvest and population changes are quite similar to the diffuse demand case. In the right-hand panel, it is clear that the harvest for all others takes a small jump upwards when the first species goes extinct. This is demand concentration. After the second extinction, there is another jump upwards, and the populations in the left panel fall faster. The pattern of harvests in the right panel looks very much like serial depletion, with slow-growing species going extinct first, and their extinction setting the stage for others in the future.

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[43]Since $SS(1)$ is finite, whereas the concentrated demand schedule approaches infinity at 1 it appears that whenever concentrated demand and $SS(z)$ intersect once, there will always be a second equilibrium as well. This is not correct: the construction of the concentrated demand schedule assumes $D(z)/[1 - z] > SS(z)$ for all $z < \bar{z}$, and this is not true for any z to the right of z_B. Therefore, concentrated demand as constructed does not exist over the entire interval.
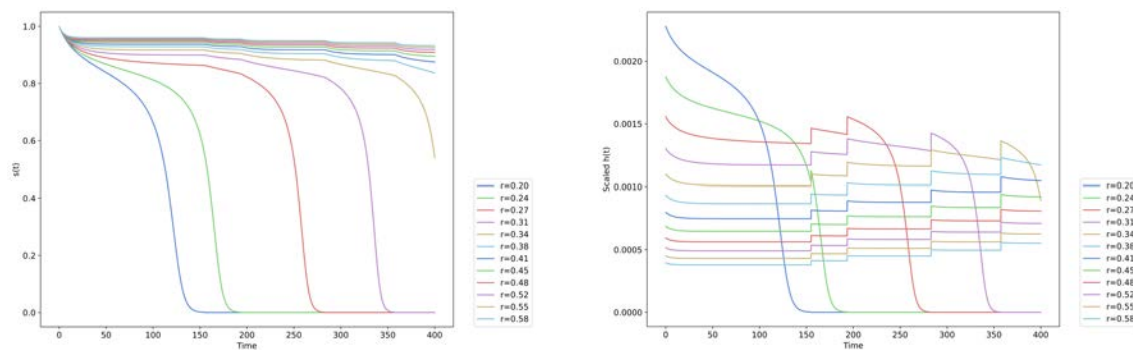
(a) Solution of the differential equation for different r values

(b) h(t) for different r values

Figure 15: Concentrated Demand with Habitat Intact

Despite demand concentration, not all species go extinct. Demand does rise with every extinction, making extinction more likely but the set of remaining species is also, on average, much faster growing. As a result, it becomes increasingly hard to generate extinction outcomes. The number of extinctions rises over time, but the time between extinctions is stationary or even increasing.[44]

VI.I.2   Slow Steady Habitat Loss

We now return to our base case of diffuse demand to examine the impact of habitat loss. In this case, we again start from our initial conditions but let the vulnerability of all species increase slowly over time. Specifically, we assume each species' carrying capacity falls slowly over time so that over a century, or 100 time periods, vulnerability is only 2.5% higher. In terms of our theory, these changes are akin to small continuous supply shocks, which shift the supply of extinctions schedule down over time. This is illustrated in Figure 16. Ignore the concentrated demand schedule for the moment to focus on the intersections of our horizontal $D(z)$ with the $SS(z)$ schedule which is slowly shifting downward. The number of extinctions grows as the potential steady states change from A to B to C, but since demand is diffuse, the impact of habitat loss appears to be relatively benign.

Our simulations in Figure 17 show exactly this: many of the species are initially doing quite well, but over time, their vulnerability rises and populations fall. As shown, seven of the twelve species go extinct in the 400 time periods. Harvests and populations fall monotonically

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[44]The literature on declining trophic values in fisheries' catch or what is commonly called "Fishing down the food chain or web", could arise from serial depletion like we show here. For an introduction to the relevant literature, see Cressey (2010).

throughout and the serial depletion - boom and bust pattern previously seen - is now absent.

Although the majority of species do go extinct, the time period between extinctions is either constant or increasing. Slow habitat loss creates slow changes in underlying populations, and again, the rapidly growing populations remaining, slow down the overall rate of extinctions. Over any short period of time, there are no abrupt changes in populations or harvesting, and the lack of dramatic spikes caused by serial depletion may well be a problem - the underlying issue may not be identified, and policy changes needed to halt habitat loss may not be undertaken.
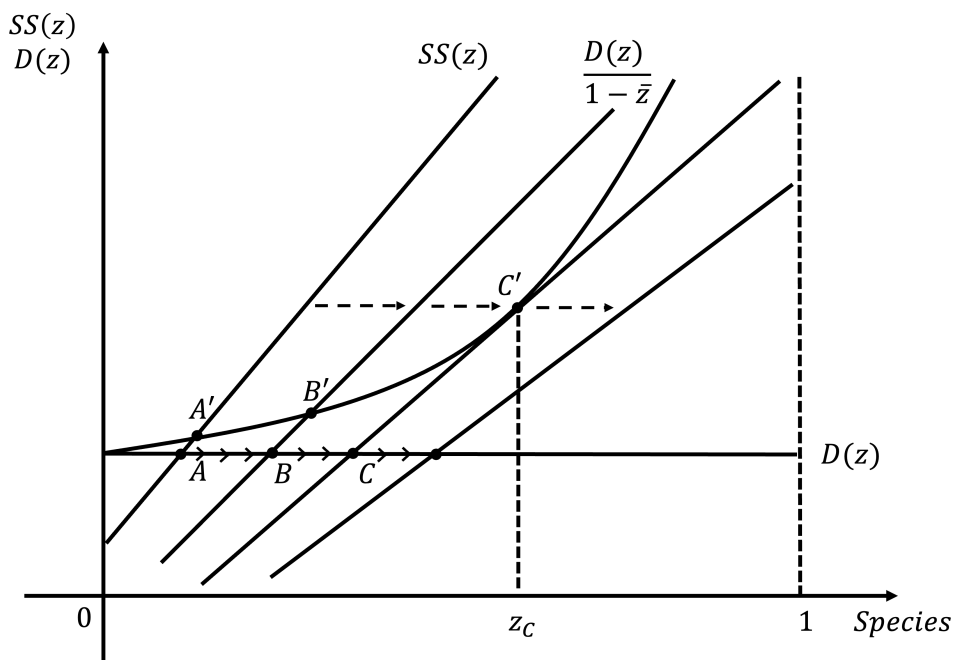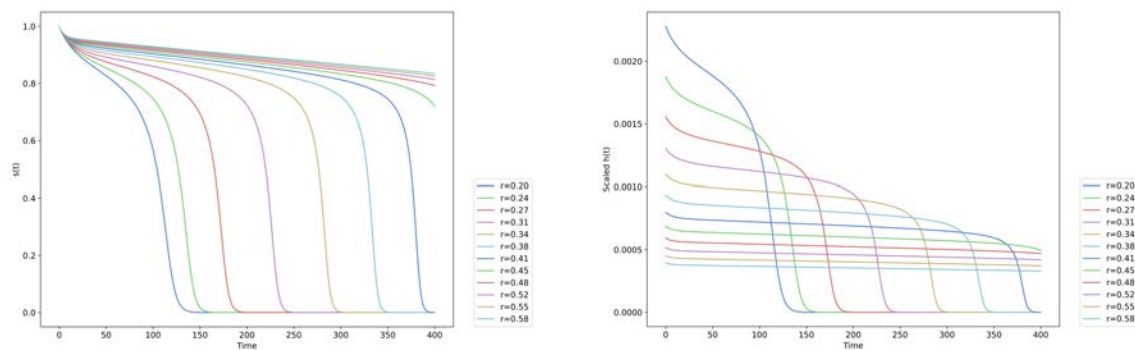

Figure 16: Gradual Habitat Loss

VI.I.3   The Ingredients for a Mass Extinction

We now combine concentrated demand with habitat loss. Perhaps not surprisingly, these two are complements in creating extinction. We show this using our theory in Figure 16. As before, habitat loss shifts the $SS(z)$ schedule downward, but now the potential steady states move from A' to B' through to C'. But large enough changes will shift $SS(z)$ further and eliminate all possible interior equilibria - all species go extinct.
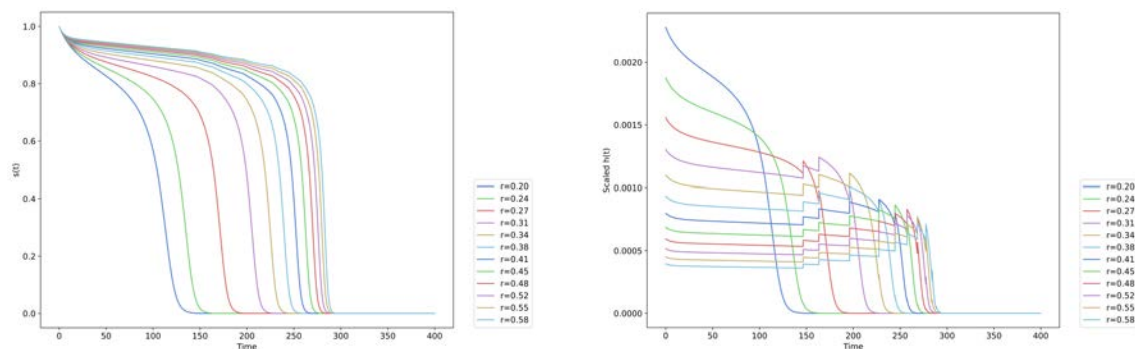
Notice that $SS(z)$ shifts downward and becomes less steep. The steepness of $SS(z)$ reflects nature's shock absorber, which limits extinctions when demand is concentrated on

(a) Solution of the differential equation for different r values

(b) h(t) for different r values

Figure 17: Diffuse Demand with Gradual Habitat Loss

(a) Solution of the differential equation for different r values

(b) h(t) for different r values

Figure 18: Concentrated Demand with Gradual Habitat Loss

fewer but faster-growing species. But when habitat loss occurs, each species is less capable of sustaining harvesting (the schedule shifts down), but the advantage of more rapid growth is also diminished in habitats that are getting smaller and smaller (the schedule gets flatter). This is an implication of equation (5), where an increase in v lowers the maximal growth rate of any species. As a result, an interior intersection becomes increasingly unlikely. And not only could all species go extinct, but the extinction rate also rises, generating a mass extinction.

This is exactly what our simulation in figures 18(a) and 18(b) shows. In this case, all twelve species go extinct. Interestingly, each of the individual species now exhibits the boom and bust pattern of serial depletion we saw earlier, but now habitat loss works in concert to increase the overall number of extinctions and compress them in time as well.

To see this compression of extinctions more clearly, we present a graph of the measured

extinction rate over the relevant period in Figure 19. The dots represent instances when extinctions occur, and joining them gives us an idea of how the rate of extinction accelerates exponentially.[45] At each extinction date, we calculate the rate of extinction per million species-year over the last intervening 100 years. As shown, the rate of extinction starts quite low, as it should. The number of existing species is large, which reduces the rate of their extinction, and the speed with which extinction occurs is slow because demand has yet to concentrate significantly. As time goes on, the set of species shrinks which raises the rate of extinction, just as demand concentration becomes much more powerful given the smaller set of remaining populations. As a result, the extinction rate spikes which produces what we might refer to as a mass extinction event.[46]
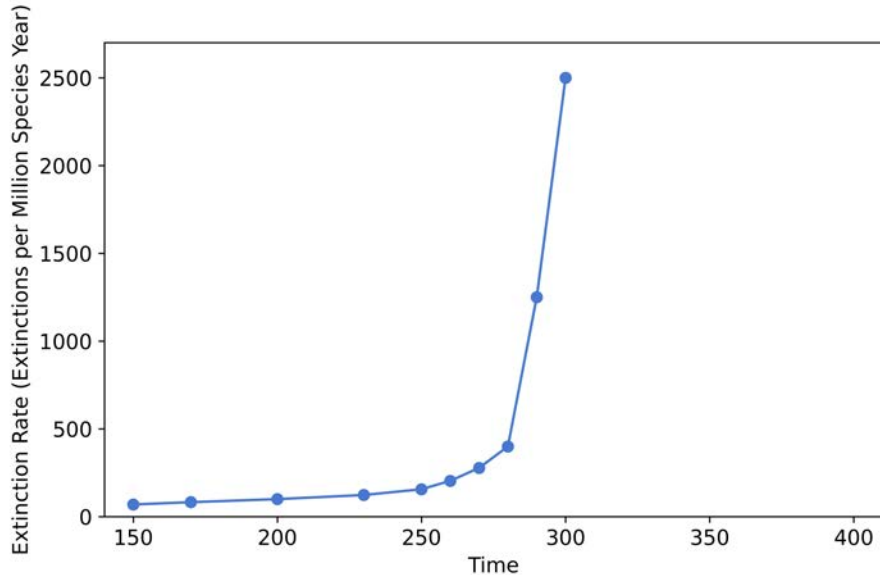

Figure 19: A Mass Extinction?

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[45]We calculate the number of extinctions occurring in a 100-year moving window throughout our simulation period. For example, let there be 2 extinctions in one such window. We define an extinction as a species population falling below M the minimum viable population - it is functionally extinct. Then the number of extinctions in this window, divided by the total number of species at the start of the window (let it be 5), times 100, tells us the number of extinctions per species year (2 extinctions per 5x100 = 500 species years). We then translate this rate into extinctions per million species years by multiplying by 2000 to find an extinction rate of 4000.

[46]The convexity of the curve is important, not the values of the extinction rate. They depend on our definition of time which we choose to be years, but we could have chosen one interval to be 100 years and then the extinction rate would be much smaller per million species years.

VII   Data Sources

Our theory shows how demand concentration and gradual habitat loss can combine to produce a mass extinction. But, of course, possibilities are not necessities, and simulations are not empirical evidence.[47] In particular, the model assumes policymakers are, at best, slow-moving or, at worst, do not regulate or restrict use despite falling natural population levels.

Shouldn't policymakers be expected to intervene to preserve species? The U.S. Endangered Species Act, in particular, is thought to have been a great success since its inception.[48] Similar acts exist in Canada, Europe and elsewhere, so does this mean policymakers often or always move quickly enough to avert extinction? Of course, good policy requires good data, and a significant barrier to action is often the availability of data. Our two case studies employed a wide array of data, but these are just two cases.[49] The question remains: are these case studies outliers, or is there evidence that many species in the world today are under the threat of extinction? We try to answer these questions by looking more deeply into two data sources we introduced in Section 2.

To do so we provide a detailed examination of what these sources say about the health of shark populations worldwide. We start with the Living Planet Index (LPI), followed by the International Union for the Conversation of Nature's assessment of individual species (the IUCN Red List). Our hope is to find that these data sources provide similar answers to questions about extinction risk, and are largely complementary in the information that they can provide to researchers and policymakers. We limit ourselves to a large - 55 from the LPI and 427 from the IUCN Red List - set of shark species because comparing the two data sources across all taxa is just too broad an exercise to be useful.

VII.I   The Living Planet Index

The LPI is a valuable resource, but it has several well-known limitations. Ideally we would like an index of biodiversity to measure the change in population abundance across a randomly selected subset of species (or higher order aggregates) living in many different habitats and countries. This would require regular, and consistently measured, stratified sampling of

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[47]A key determinant of whether we can generate a mass extinction is a comparison between how fast $r(z)$ increases with z, relative to the rate at which demand concentrates. In our simulation, we have assumed $r(z)$ is a linear function, whereas demand concentrates by shifting budget shares, which makes the demand side convex in z. Not all parameterizations of the model lead to a mass extinction event.

[48]See the discussion in "The Endangered Species Act at 40" (Jan. 16, 2014, in *Nature*).

[49]Several others are contained in Kolbert (2014).

species worldwide. Not surprisingly this is not how the data is collected. Instead the data is collected opportunistically from primary sources: scientific studies, community reports, volunteer counts etc.[50] As a result, the species, time periods, populations, geography, etc. of the data collected is far from a random sample; moreover, the primary data sources differ greatly in both their quality and the units of measurement used.

One very natural worry is that selection may be biased towards endangered populations. To evaluate this, researchers compare the number of species within a certain taxa in the data vs. this same ratio in the wild. Collen et al. (2009) for example finds the index is heavily reliant on bird population counts, has sparse coverage of tropical species populations vs. those in temperate regions, but may not to be disproportionately sampling endangered populations. The evidence for no bias towards endangered populations is however weak, since many taxa are very poorly represented in the LPI data. One class well represented is Mammals, but the proportion of all mammal species in the LPI that are critically endangered or endangered is twice the proportion they appear in the wild: they are over-represented.[51] Broadly similar concerns were raised by Marconi et al. (2021). They construct an LPI specific to Canada and report a 10% decline over their sample period 1970-2014, but when this data is disaggregated the authors find trends for species with poor data quality are much more negative than those for species with better data quality.

A second data issue arises because the primary studies underlying the index, measure populations in different units. A primary study for example may measure the density of bird nests in a given area over time rather than the observed bird population. A similar study may instead report bird counts for a different population of the same species. To combine these data, the data on abundance (in any unit) is used to calculate yearly percentage rates of change (that are free of units). These rates of change are then simply averaged to obtain the average change for this group. This average rate of change is then applied to the group's index to generate a level change in the index.

This procedure reveals two things. First, it tells us that *changes in the index do not measure the change in the underlying population for any species or higher aggregate.* Movements in the index reflect the average rate of change across a group, and nothing more. Therefore, a declining index tells us that, on average, this group's population growth rates were negative

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[50]These sources range from articles in refereed scientific journals to unpublished reports. The data contained in these sources range from actual population counts to expert judgements about population sizes.

[51]See Table 1 in Collen et al. (2009) for a comparison of the frequency of a species being in the LPI vs. listed in the IUCN Red list.

- it does not tell us the populations overall declined.[52]

Second, since movements in the index are driven by the computed arithmetic average of growth rates, the index is greatly affected by outliers. Very large or very small growth rates will have a large influence on the group average and, hence index. This is problematic because even small absolute changes in populations have large implications for measured growth rates when populations are small.[53]

A third challenge is that populations with as little as two years of observations are included, there are spans of missing data as long as twenty years that need to be filled by a smoothing procedure. As a result, intervening years are estimated and interpolated, and the interpolated data and resulting growth rates are treated in exactly the same way as we would real observations.

A final critique comes from Buschke et al. (2021) who shows that (mean-zero) variation in population estimates are sufficient to produce a declining index despite the fact that the population is, in fact stable. Therefore in a world with stable populations subject to random fluctuations, the LPI declines. Similarly, classical measurement errors would have the same effect.
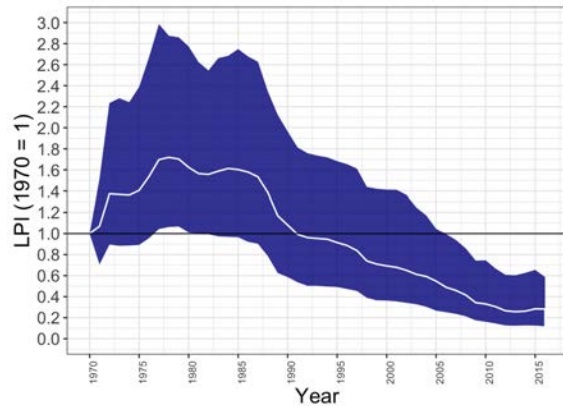
As a result of these challenges and critiques, it is unclear what changes in the LPI really mean. And therefore, should we be alarmed about the trends shown in Figure 3(a) and 3(b)? To understand the mechanics and limitations of this very important measure we decided to test it ourselves. We collected from the LPI all of their publicly available data on shark species. The data spans the period from 1950 to 2018 and includes 284 total time series of abundance measures spread across 63 shark species. 231 of these series are uninterrupted series meaning there are no missing data within the time series; while 53 time series are interrupted (had missing values). The data is far from a balanced panel: of the almost 20,000 population abundance x years observations (69 yrs × 284 series), there is data in only 18% of these cells, with 82% therefore missing. Even if we take the post-1970 period forward, this coverage improves to only 23%. Finally, the data is measured in a dizzying array of units: from indirect measures of abundance such as catch per unit effort to the average number of sharks per tour recorded by cage divers on through to numbers of aerial sightings per 100

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[52]For example, suppose one time series showed a robin population of 100 rising to 105 - a 5% increase; while the other showed a robin population of 5 falling to 4 - a 20% decrease. The average growth rate used in the LPI would be (-15%/2) = -7.5%, but the robin population overall grew from 105 to 109.

[53]Suppose again that one robin population went from 1 to 2, while 4 other populations of 100 birds each went to 105. The calculated average growth rate for these robins is then $(4 \times 5\% + 100\%)/5 = 24\%$, which is very misleading about the change in the robin population. Since small populations are more likely to exhibit large positive or negative changes, averaging growth rates gives outliers tremendous weight.
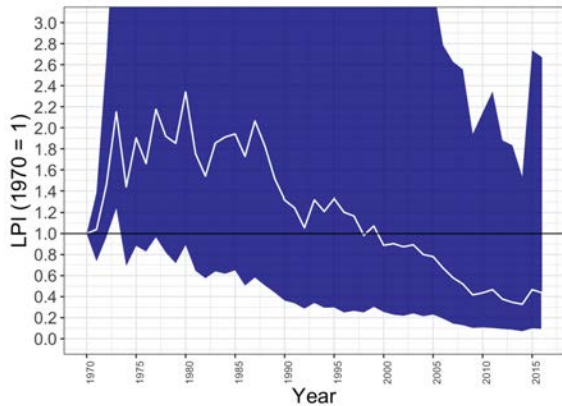
(a) The Raw Data LPI (1970 to 2016)   (b) The Smoothed LPI (1970 to 2016)

Figure 20: Living Planet Index

sq km. In fact, there are 107 different units of measurement and 126 different measuring methods across our 284 time series! Even though these methods must differ greatly in the accuracy of their estimates, no allowance is made for this in the LPI.

Given the different data collection methods, it is unsurprising that the LPI must escape their unit problem by calculating annual growth rates for each measure of abundance. These annual growth rates are first smoothed across time but within populations (to fill in holes and smooth) and then averaged across populations within species for a given year. This generates a time series of (smoothed) species-specific growth rates. These species averages are in turn, averaged across all species within a given higher aggregate, such as their genus. This growth rate is then applied to the index number to determine it path over time.

We replicate their methods here and construct our own LPI-type index for sharks. To do so we start by trimming the data: we exclude all interrupted series, and we start in 1970 and end in 2016. Even with this trimming the number of (uninterrupted) populations reporting any data for a given year varies tremendously from 19 in 1970, then growing to 105 in 2003, only to fall again to 22 in 2016. Therefore, the composition of the index changes radically over time. Following the LPI procedure, but without smoothing, the index we create from a now reduced 55 shark species is shown in Figure 20(a) together with the same index but now calculated with the LPI smoothing procedure.

Three features are of note. First, both indices rise from their base year of unity in 1970 to eventually fall. However the raw data index in 20(a) remains above unity until year 2000, and at the end of the period the index has fallen to .6 - or a 40% decline. In contrast the

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smoothed series in 20(b) falls below unity in 1991 - almost ten years earlier - and by the end of the sample, it is at .2 - indicating a 80% decline! The smoothing procedure has a large impact on the results. The smoothing procedure used in the LPI is a form of general additive modeling. It is used to both smooth the pattern of growth within existing and complete data series and provide estimates to fill in observations for incomplete series. We have deliberately chosen our data to be a complete series and hence isolate the role of this smoothing procedure.

Second, the dark regions in panels (a) and (b) are constructed 95% confidence intervals derived from a simple bootstrap procedure. As shown, the region in panel b) is large, admitting not only the raw data LPI we constructed in panel a) but also many others. The very large bounds on the bootstrapped intervals come from the very large variance in growth rates at any point in time and show quite clearly the role that outliers can play in determining the index values.

Third, in panel b) there appears to be a narrowing of the confidence interval in later years of the sample, making the LPI index perhaps a more accurate representation of population changes. The natural tendency is to read the narrowing blue region as increased precision arising from observations growing over time. This interpretation is entirely wrong. The precision shown in later years comes from the very small number of observations in those years rather than the reverse - it is very difficult to have large outliers when your very few data points are drawn from only a handful of studies.

Finally, despite these significant differences, the two indices do agree that average growth rates for sharks have been negative for many years - perhaps since 1985 or 1990; the decline has been quite dramatic overall - somewhere in the range of a 40-80% decline since 1970; and, there is no evidence of the trend reversing itself. However, given the limitations and noisiness of data the confidence intervals are immense. We need further evidence before declaring sharks, in general, in peril.

VII.II   The IUCN Red List

For our analysis the three most important categories in the IUCN Red List are VU, EN and CR. The criteria determining the classification for a given species are the speed of its population size reduction (past, present or projected); the geographic range, size and fragmentation of its habitat; the size, fluctuation and distribution of its very small population

or sub-populations; and a quantitative analysis of its risk of future extinction.[54] In terms of our theory, these are $\dot{S}$, K, S with extinction risk rising in v for any species. For example, if S/K is close to v the extinction risk must be very high.

Vulnerable (VU) are those species that possess a high risk of extinction as a result of rapid population declines of at least 30% over the last 10 years or 50% over the last three generations. These reductions or their causes may not have ceased, be understood or be reversible. Other criteria include a relatively small population size (fewer than 10,000 mature individuals), a small geographic range (less than 20,000 km2) and a probability of extinction of at least 10% within 100 years.

Endangered (EN) species possess a very high risk of extinction as a result of rapid population declines of at least 50% over the last 10 years or 70% over the last three generations. Again, the reduction or its causes may not have ceased, be understood or be reversible. Other criteria include a relatively small population size (fewer than 2,500 mature individuals), a small geographic range (less than 5,000 km2) and a probability of extinction of at least 20% within 20 years or five generations.

Critically Endangered (CR) applies to those species that possess an extremely high risk of extinction as a result of rapid population declines of at least 80% over the last 10 years or 90% over three generations. The reduction or its causes may not have ceased, be understood or be reversible. Other criteria include a relatively small population size (fewer than 250 mature individuals), a small geographic range (less than 100 km2) and a probability of extinction of at least 50% within 10 years or three generations.

According to the IUCN Red List, there are more than 42,100 species in these three categories and thus threatened by extinction (28% of all assessed species) in 2023.[55] For birds, the share equals 13%, for mammals 27%, for sharks and rays it is 37% and for amphibians it is estimated to 41%. Note that these shares are likely to be biased in some direction as the choice of species being assessed for the IUCN Red List is endogenous: it depends on the willingness, capability and feasibility of experts and sponsors to perform and provide assessments. IUCN emphasizes that the assessment is biased towards terrestrial and, in particular, forest ecosystems with a better coverage of animals. And even if the goal of 160,000 assessed species will be reached, this equals less than 10% of the 2 million described species we currently know of, and we have given scientific names.[56]

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[54]Note that only one of these criteria needs to be met to the required degree in order to qualify for a certain category. See IUCN (2022), particularly Table 2.1., for the criteria and classifications.

[55]See https://www.iucnredlist.org/.

[56]Walsh et al. (2013) emphasize that lists of threatened species are typically biased towards charismatic

	In the Data Set		Current Population Trend			
	# of Species	ln %	# of Species with data	ln%		
				-	=	+
Category	(1)	(2)	(3)	(4)	(5)	(6)
CR	35	8%	33	100%		
EN	50	12%	50	100%		
VU	68	16%	65	100%		
$\sum$	153	36%	148	100%		
NT	37	8%	36	97%	3%	0%
LC	237	56%	150	3%	91%	6%
$\sum$	274	64%	186	21%	74%	5%
$\sum\sum$	427	100%	334			

Source: Own analysis based on the IUCN Red List

Table 2: Risk of Extinction of Shark Species on the IUCN Red List

To see how well the data provided by the IUCN matches the conclusions a researcher may make from the LPI, we conducted our own analysis of all the sharks within the "Chondrichthyes" class of the IUCN Red List. Fortunately, the IUCN Red List includes an impressive amount of information on current and past assessments and observations on each species, which we present in Table 2 below. Our compilation of the IUCN data from their homepage revealed an available sample of 427 shark species.

The first column of Table 2 shows that of our 427 shark species, 153 species (36%) are considered to be threatened by extinction (in the top three categories CR, EN, and VU), whereas 274 (64%) are classified as "near threatened" (NT) and "least concern" (LC). These numbers seem broadly consistent with the trends observed in the LPI, although these entries represent a snapshot in 2023. To understand population changes, we report in column (3) the number of species with data on their current population trend from the IUCN Red List. Sharks for which we can find information on their current population trend represent 334 of our original sample of 427.

We report in columns (4)-(6) whether these population trends are either negative, neutral

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fauna and flora, whereas Possingham et al. (2002) generally question whether these lists should be used as a basis to prioritize species recovery and habitat protection.

or positive. Column (4) shows that sharks in all of the three top three categories exhibit negative population growth rates (recall their definitions), but surprisingly, so too do 97% of the near-threatened sharks. If we proceed further to the least concerned group of sharks, only 6% of these sharks have positive growth. Or alternatively, only 9 sharks out of the 334 sharks for which we have information on their current population trend exhibit positive growth. Sharks overall - not just those currently endangered, vulnerable or critically endangered - are declining in numbers. It is rare to find a shark population rising. This evidence is not proof that a wide range of sharks are heading towards extinction. Rising demand or reduced natural supply would also lead to negative growth rates for a broad range of shark species, even if very few of them were destined for extinction.

To investigate further, in Table 3, we present an alternative way to capture the over-time variation in shark populations. We now focus on the assessment of a shark's overall risk of extinction and ask whether and to which extent the risk category (from LC to CR) of an individual shark species changed over time. In column (1) we report the number of sharks with useful data from past assessments. Since not all sharks have past assessments, our data now covers only 231 of our previous 427 species. We then report how a species listing has changed over time. For example, consider the group of 24 critically endangered sharks with past assessments. Of these 24, 18 shark species transitioned into CR from a lower risk category in their last assessment, while 6 remained in the CR category they were assessed at previously. No species of sharks moved to a lower risk category.[57] Column (4) alone shows that improvement in a classification for any shark species - even those of least concern or near threatened - is rare. And if we limit ourselves to sharks in the top three risk categories, only 3 saw improvement from their last assessment.

More generally, Table 3 reveals a pattern of shark species moving up to categories representing a higher risk of extinction. That is, by comparison of their growth rate, population size, distribution, state of habitat or fluctuation, which determine their risk category across assessment periods, these species appear *increasingly* threatened. This pattern fits well with the trajectory of a species on an extinction path - its growth rate must become increasingly negative over time. To see the extent to which sharks follow this pattern, compare columns (2) and (4). The share of shark species that transitioned to a higher risk category is considerably greater than the share whose classification improved. For example, 75% in the CR

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[57]There is one species, the so-called "Lost Shark" or Carcharhinus Obsoletus, which is reported as "last seen in 1936". Nevertheless, this shark has been assessed for the first time in 2020 and put into the CR category (and not into the extinct (EX) group).

	Species with Past Assessments	Change of Category Over Time (Now vs. Past)		
	# of Species With Data	Higher Risk Category	Equal Risk Category	Lower Risk Category
Category	(1)	(2)	(3)	(4)
CR	24	18 (75%)	6 (25%)	0 (0%)
EN	30	24 (80%)	6 (20%)	0 (0%)
VU	45	23 (51%)	19 (42%)	3 (7%)
$\sum$	99	65 (66%)	31 (31%)	3 (3%)
NT	21	6 (29%)	15 (71%)	0 (0%)
LC	111	XXXXX	98 (88%)	13 (12%)
$\sum$	132	6 (4%)	113 (86%)	13 (10%)
$\sum\sum$	231			

Source: Own analysis based on the IUCN Red List

Table 3: Risk of Extinction of Shark Species on the IUCN Red List

category moved from a lower risk category, whereas 0% transitioned to a lower risk category. 80% of the endangered category EN moved to a higher risk category, and 0% improved. 51% in the VU vulnerable category moved to a higher risk while 3 (or 7%) improved. Even for the species in the category NT, the share is 29%. In the lowest risk category LC, this comparison is impossible as there is no lower category to compare with.[58]

Overall, the results from the IUCN paint a similar picture to that of the LPI index. The LPI index provides us with evidence that growth rates for sharks, on average, are negative and have been negative for some time. It tells us nothing about populations per se, and the confidence intervals surrounding these estimates are very large. Here, the IUCN data is key since it is based on population assessments and also accounts for habitat loss. The IUCN data shows only 9 shark species, of the 334 with population growth data, have recorded positive

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[58]Although some shark species in the LC category are likely to show up in a higher risk category in future, the fact that 88% of the sharks with previous risk assessments in this category were in the same category offers us some solace. Unfortunately, while most of the assessments (approximately 90%) are very recent and conducted in the last four years, the data on the assessment of sharks in the LC category is much older. More than 40% of this group have assessments older than 4 years, and hence it is difficult to know whether more current assessments might push a large number of these species into higher risk categories. Also note that for the shark species in the categories VU, NT and LC, there are quite a few for which a past assessment implied "DD" (=Data Deficient). These species are not included in Table 3 for obvious reasons.

population growth. The vast majority are in decline. In this sense, the IUCN data and the LPI data are complementary. The LPI covers far more years, but the IUCN methods are more transparent.

The most useful component of the IUCN data is thus the reported change in listing. First, we note that 65 of the 99 shark species in the top three at-risk categories (all of which have negative population trends) have transitioned into a higher-risk category. That is, these 65 sharks' growth rates have either fallen further (consistent with an extinction path), or their populations have become perilously low (closer to our M). Analyzing the 18 shark species of the CR category that moved up from a lower category in the most recent assessment, it turns out that more than half of them (11 species) were pushed up by more than one risk category compared to the previous assessment. Similarly, 9 species of the 24 in the EN category that originates from a lower-risk category also moved up by more than one category.

Second, we determine whether the speed toward extinction has increased by focusing on 5-year increments between 2000 and 2020. Figure 21 reports the cumulative fractions of shark species per group (VU, EN, CR) with an increase in the extinction risk category. The figure is constructed to be similar to our Figure 2 drawn from Ceballos et al. (2015).[59] We normalize the number of sharks that jump up at least one category in a 5-year window by the total number of species at the beginning of the window for which we have information on their extinction risk (excluding DD). We then sum these fractions over past periods to show the cumulative function. Figure 21 implies that the fraction of shark species moving to a higher extinction risk category rises for each group over time with a sharp increase in the last period; this is also true for all shark species in the three groups together ("Total").[60]

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[59]It is similar to Ceballos et al. (2015) in that we calculate the cumulative function in % of the IUCN-evaluated species; it is different in that we focus on the changes in the risk category of existing species within 5-year increments (and not on the extinctions within 100-year periods) and that we calculate simple fractions (and not changes per 10,000 species per 100 years).

[60]The IUCN cautiously distinguishes between "non-genuine" (N) and "genuine" (G) reasons for a change in the Red List categories which are reported in the so-called Table 7 (https://www.iucnredlist.org/resources/summary-statistics, accessed on November 7, 2023) for individual species. In IUCN (2022), the Species Survival Commission explains that "Many category changes result from a combination of improved knowledge and some element of genuine deterioration or improvement in status" (p. 13). This also applies to the shark species we use as a basis for our analysis in Table 3 and Figure 21: It turns out that three-quarters of the 99 shark species in the CR, EN and VU categories we use are labeled with an N and only 6 sharks (6%) with a G; for 17% the information is lacking. A separate analysis of the small set of sharks for which IUCN reports a genuine reason (G) for the change of classification (all of which are in the EN group), however, implies qualitatively the same result as for the rest of the species in this group regarding the dynamics reported in Figure 21. Given this result and the descriptions in the individual assessments of sharks in the IUCN Red List, we trust that these re-classifications provide an accurate picture of these shark species' trajectory towards a possible extinction.
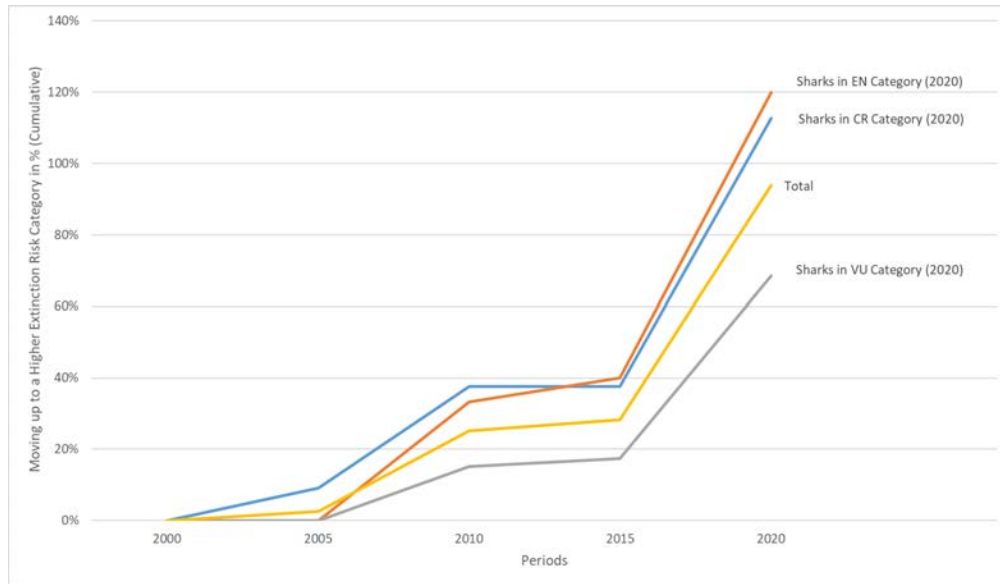
Figure 21: Increase in the Extinction Risk Category of Shark Species per Group and 5-Year Increment (2000-2020, Cumulative in %)

VIII   Has Protection been Forthcoming?

While our analysis of shark populations is not exhaustive, the evidence gleaned from our test case using the LPI and the IUCN Red List points in the same direction. Many shark species are headed towards extinction. Average growth rates for shark populations are negative (the LPI) and have been for many years; the IUCN data shows population numbers are almost universally declining; and the time path of at-risk category changes within the IUCN tells us that a greater fraction of shark species are at a greater risk today than they were in the past - there appears to be an acceleration. This evidence is consistent with our theory of multi-species extinction when demand concentrates on remaining species, and ongoing losses of reef habitats from bleaching or pollution discharges accelerate the process. The result may be that a significant number of sharks go extinct in a (geologically) short time, which would have potentially serious knock-on effects on many ecosystems.

Removing predators typically has a first-order effect on prey species but can also alter other relationships within an ecosystem. These effects are hard to predict ex-ante and often cause trophic cascades as abundance changes for several species. Stevens et al. (2000) argues that shark extinctions will create unexpected outcomes for tuna and jack populations; Field et al. (2009) argue that extinction lowers ecosystem resilience and ushers in destabilizing trophic cascades, while Dixon and Gallagher (2023) go further to argue that the Tiger

Shark, in particular, may play an important role in safeguarding the blue carbon ecosystem which supports carbon sequestration in the ocean floor. At the very least, extinctions of top predators bring very uncertain changes to the ocean environment.[61]

It is natural to ask how policymakers have responded to what is plainly obvious in the data. Given the role of international trade in their depletion, it is reasonable to start by asking about the protection CITES has provided.[62] The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) is the oldest environmental treaty in the world. It was established in 1973, long before sharks were in trouble, and covers almost all producing and consuming nations of the world (as of 2023, there are 184 Contracting Parties, 183 countries, and the EU). Therefore, CITES has the experience and breadth of country coverage to monitor the world's trade in shark fins and intervene if necessary.

VIII.I   Evaluating Current Policy

To evaluate the policy response, we focus on protections afforded to the set of shark species we studied in our test case. These protections, if afforded, list a species on one of three appendices of CITES (I, II, and III). Whereas only the Conference of the Parties (CoP) can amend Appendix I and II, individual countries can add or remove species from Appendix III by notifying the secretariat of CITES. Note that a two-thirds majority of parties who are present and voting is sufficient to, for example, add a species to Appendix I or II during the CoP, which typically takes place every three years. However, members do have the opportunity to enter a reservation with respect to an amendment if they do not agree with a decision. Moreover, party-specific listings are possible.[63]

Species listed on Appendix I are the most endangered and their trade is prohibited except when the purpose of the import is not commercial.[64] Currently, it includes 1099 species (704 species of fauna and 395 of flora). Appendix II includes species "that are not necessarily now threatened with extinction, but that may become so unless trade is closely controlled". Whereas international trade in species on Appendix II only requires an export or re-export permit from the country of origin to be presented when being imported to another country,

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[61]See the very interesting article by Estes et al. (2011) relating extinctions within an ecosystem to consequent changes elsewhere in the system.

[62]CITES includes over 40,900 species – 6,610 species of fauna (animals) and 34,310 species of flora (plants) – which, according to CITES, "are protected by CITES against over-exploitation through international trade". See https://cites.org/eng/disc/species.php.

[63]See Art. XXIII of the CITES Convention and the simultaneous listings for some species on the appendices.

[64]See https://cites.org/eng/app/index.php, including the linked "Text of the Convention".

species on Appendix I are banned from trade by both exporting and importing countries. Appendix II currently includes the greatest number of species (39,230 of which 5,466 are animal and 33'764 are plant species). Lastly, species in Appendix III are monitored "at the request of a Party that already regulates trade in the species and that needs the cooperation of other countries to prevent unsustainable or illegal exploitation". Importing countries are asked to monitor the import of these species by checking the origin of the specimen of a species and, if it originates from the country that included the species in Appendix III, to require the presentation of an export permit. Appendix III currently includes 506 species (372 species of fauna and 134 species of flora). In all cases, enforcement is carried out by the law enforcement authorities of the individual members, though international trade sanctions can, in principle, be implemented against parties that fail to implement CITES regulations (Vincent et al. (2014)).

Clearly, CITES has several ways to protect shark populations. However, until recently (December 31, 2022), only 15 shark species were covered by a CITES listing, and all 15 of these species were listed in Appendix II. This is true despite the fact that three of the 15 shark species listed are critically endangered, according to the IUCN; five are endangered, and six are vulnerable to extinction. The remaining shark species listed fall within the IUCN data deficient category. Therefore, there is an alarming gap between what the LPI and IUCN data tell us about the precarious situation of many shark populations and the extent of protection they are afforded in CITES. If we now ask how many shark species fall into high-risk IUCN categories but receive no protection from CITES, the picture is even worse. Using the data in Table 2, we find that 32 of the 35 critically endangered sharks were not listed on any appendix; 45 of the 50 endangered sharks were not listed; and 62 of the 68 in the vulnerable category were not listed either.

Very recently, in May of 2023, CITES added 59 shark species to Appendix II, raising the number of listed sharks to 74. However, it is important to remember that an Appendix II listing does not ban trade in a species but requires an export permit to be controlled by the importing countries and some reporting duties (that nations may not meet). For example, Cardeñosa, Merten and Hyde (2019) emphasize that, in the case of sharks, many member countries do not meet their reporting obligations, nor do they comply with the CITES regulations despite the small numbers of sharks listed in Appendix II at the time of investigation. Similarly, in their "Missing Sharks Report", Okes and Sant (2022) found "lack of transparency" and thus poor reporting by a relatively large number of countries with respect to the CITES-listed sharks.

Moreover, the coverage of these listings is still rather incomplete. If we refer back to the IUCN Red List, we find 63% of the critically endangered sharks are still not listed, 62% of endangered sharks are still not listed, and 65% of those sharks vulnerable to extinction are not listed. This is the case even though our reading of the IUCN's assessment reports of these individual shark species, particularly of those in the top two risk categories, leaves little doubt that international trade is a driving force behind the population declines of many of these species.

In addition to these efforts by CITES, there are many other agreements designed to limit shark hunting worldwide (see, e.g., Shiffman and Hammerschlag (2016) for an overview). The "International Plan of Action for Sharks" was adopted by the UN FAO Committee on Fisheries in 1999 with the suggestion that the shark fishing nations include the content in their "National Plans of Action for Sharks." The "Memorandum of Understanding on the Conservation of Migratory Sharks" (a daughter agreement of the Convention on Migratory Species by the UN Environment Program) has been created in 2010. A whole network of "Regional Fisheries Management Organisations" has been established to govern fishing operations on the high seas and thus for populations that move between exclusive economic zones. Examples are the "Western and Central Pacific Fisheries Commission" or the "Northwest Atlantic Fisheries Organization" that each include a significant number of countries and provide their own regulatory framework (e.g., regarding finning). Finning restrictions and finning bans have also been put in place by a number of countries (Grimes (2018)). For example, in 2021, the U.S. Senate introduced the Shark Fin Sales Elimination Act, a nationwide ban on possessing, buying, selling or transporting shark fins.[65]

Many projects have been initiated and many agreements signed over the last 30 years to reduce the over-harvesting of sharks. In addition, organizations such as "WildAid" or "Shark Truth started campaigns in China and other countries years ago to raise awareness of the negative consequences of shark-fin-soup consumption. However, the data shows these many actions have yet to turn the tide for shark populations worldwide. One small bright spot is a recent reduction in landings, but these changes may reflect reduced fishing productivity because of smaller populations rather than improvements in fisheries management (Davidson, Krawchuk and Dulvy (2016)).

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[65]See www.congress.gov at "S.1106 - Shark Fin Sales Elimination Act of 2021".

VIII.II A Path Forward

The greatest threat to effective species protection is probably data deficiency. One step forward would be for countries to establish a country-wide biodiversity census, using methods and procedures employed for the population or census of manufactures. We cannot save what we do not count, and the patchwork of existing data created by researchers, government scientists, and others is not up to the task. Saving biodiversity is expensive: it requires major changes in the perception and behaviour of mankind. No government or its citizenry should be asked to allocate funds based on poor information. While tremendous expenditures are often allocated to saving endangered species, the more mundane task of cataloging and counting the less charismatic species on regular five-year intervals may be more important. The census would also have to include information about the size and fragmentation of habitats, which seems to be crucial in its interaction with population size and growth, as implied by our multi-species model to study (mass) extinction.

A second major threat comes from the political process, where trade-offs across economic issues and short political lifetimes make expensive species preservation a hard sell. Economists long ago realized that politicians have a short-term interest in accepting higher inflation in order to spur temporary economic expansion. As a result, societies in many countries took monetary policy out of the hands of politicians and transferred it to their separate and largely independent central banks. Perhaps the institutions guiding species preservation also need an element of insulation. One possibility would be to adopt a system of automatic listing of species on Appendix II or I of CITES if the species in question reaches an agreed to level of endangerment as determined by the IUCN. Automatic listing on the basis of scientific information provided by a third party, can be a useful form of insulation and speed response times.[66]

Many shark species that slowly found their way to Appendix II of CITES, may indeed qualify for listing in Appendix I on the basis of their IUCN listing (see Vincent et al. (2022)). Even if automatic listing was to occur there is already in place a procedure for exceptions to Annex requirements. For example, a CITES listing is species-specific but constrains the actions of all countries. In some cases, individual populations of the species at risk may be very well protected and even thriving in some countries but not others. In cases like this,

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[66]It is common for government agencies involved in endangered species protection to have some insulation from political and economic machinations. For example, the listing of a species under the Endangered Species Act (ESA) of the U.S. has to be independent of potential future costs of preservation, and any valuation of the species itself. See Westwood et al. (2019) for a discussion of this design issue in the context of proposed species at risk legislation in British Columbia.

CITES has allowed individual countries or projects to escape trade bans to exploit small and carefully controlled experimental markets for an otherwise banned good. These exceptions could of course remain, but now the status quo would be immediate protection from which exceptions could be granted.

Automatic listings would also bring quicker response times. This may be key to species preservation. Many populations have minimum viable sizes, below which extinction is but a formality. But the existing political process within CITES is slow. The lengthy (political) process of CITES until a species is listed on Appendix II, described above and further analyzed by Friedman et al. (2020), is a good example. Would CITES have helped the buffaloes whose hides were exported to Europe in the 19th century? Probably not—the required reaction time would have been much too short for CITES. Even in the case of sharks where the decimation of populations takes much more time, there is a large lag between the reaction by CITES and the evidence on the risk of extinction provided by the IUCN Red List (and trade data).

The last key threat to species preservation is how humans view other species. For some of us, the value of other species derives completely from the desires and wishes of humans. They have value because they provide us with food, clothing, and medicine, or provide us with wonder and awe in their presence or in many different forms of art. However, the use-value of harvesting and the non-use value of tourism or art appreciation spring from human valuation alone. If we adopt this viewpoint, species should be protected if this affords us greater benefits than the attendant costs. Benefit-cost ratios would rank species, and limited budgets could be allocated accordingly. This view is so commonplace that it is difficult to see how anything else makes sense.

An alternative view of our relationship with other species is sometimes referred to as a rights-based view. For someone holding this view, all forms of life on earth have an intrinsic value and right to existence independent of any valuation we homo sapiens may place on them. This view is often associated with animal rights groups, but it also reflects the mores of many indigenous cultures. Harvesting from the earth is necessary, but our primary responsibility is stewardship.

These two views and their implied preferences spring from deep-seated philosophical differences that cannot be easily bridged. Any movement from one to the other alters property rights, shifts economic well-being, and may be zero-sum. Change, if it does come, will alter citizens' demands for species protection and preservation. But social change is typically slow and probably too slow for many of the world's most endangered species.

IX Conclusions

Every undergraduate in economics should know that in a poorly regulated economy, environmental destruction and species loss can follow from economic expansion. This is particularly the case with open access or, in other words, commonly held resources. Our simple model illustrates this basic fact by showing how the primitives of biology, the strength of underlying human demands and our impact on natural habitats interact to determine long-run population sizes. In a world with active policy, less extreme outcomes can arise but active policy is not a panacea. Monitoring problems, political constraints and species mobility can hamstring, or at least delay, effective policy responses. Without meaningful restrictions, our two case studies bluntly illustrate how supply or demand shocks can usher in rapid species decline.

The Buffalo case, in particular, was breathtaking in its speed and magnitude, earning itself the moniker *Slaughter on the Plains*. But since the buffalo case study may not be representative, we turned to examine a contemporary slaughter - that of shark species worldwide. Sharks are, of course, less charismatic than buffalo and are not an iconic species emblazoned on currency or national park signs, but they are majestic creatures who play an important role in reef ecosystems. Here we found a scale of killing that dwarfs that of the buffalo, with tens of millions of sharks killed every year for their fins and meat. Since this harvesting may not be sustainable, we expanded and deepened our discussion to include an empirical evaluation of the health of more than 500 shark species within the Chrondrichthyes class.

Evidence drawn from the Living Planet Index and the IUCN Red List are in broad agreement despite their incommensurate methods: the majority of shark species are in imminent danger - because their existing population sizes are already low, because their population growth rates are decidedly negative or because their habitats may be impaired. And if one species of sharks is easily substitutable for another in consumption, our theory of concentrated demand predicts a pattern of sequential extinction present in the data. Not protecting one shark species today, makes it harder to protect others in the future.

Whether this is the likely future for many of the world's other 10 million species is impossible to say - there is just so much we do not know. The IUCN Red List, for example, contains assessments for 150,300 species with a goal of 160,000, but this is far shy of the over 10 million species worldwide. The LPI data is a useful complement to the IUCN, but it comes from opportunistic sampling of high- and low-quality sources. The LPI method of index construction is also problematic because it conflates a declining index for a fall in

(aggregate) population sizes. With such limited data, theory has to bear a larger burden. Our theory does show how ongoing habitat loss increases the vulnerability of any species, which raises the likelihood of extinction even absent human harvesting. And when habitat loss is combined with harvesting demand concentration, it produces the serial extinction of several species that are compressed in time - it produces a mass extinction event.

It is clear that restricting or eliminating harvesting pressures on endangered species is possible and may be relatively easy - the success of endangered species legislation in some countries has shown us this - but forestalling habitat loss created by climate change is difficult, if not impossible. And the same fragmentation of natural habitats by roads, rail and pipelines that makes species vulnerable to extinction is also the natural consequence of successful development. Since most of the world's remaining biodiversity lies in a narrow band of relatively poor countries around the equator, pressures on the world's remaining species will only increase over time.

These pressures which are closely linked to the patterns of past industrialization, rising human populations, and expanding infrastructure, and are already evident in recent studies showing a heightened and even accelerated rate of extinction over the last 100 years. While these studies makes clear our current predicament, predicting a future mass extinction based on the extrapolation of current trends is very risky. Homo sapiens are, after all, the dominant species on this planet. It was inevitable that we would transform much of it to suit our needs. We hunted some species to extinction and fragmented or eliminated the habitat of many others. Our curiosity led to travel and trade, which brought invasive species to new lands, sometimes with ill effects. But most of these changes occurred in the developed world and were not inevitable; they were brought about by our choices, albeit some of them poorly informed.

These choices reflect the unique ability of Homo Sapiens to see a world different from our own and then shape the future to our will. The question facing us today is whether we will use this ability to help the remaining species-rich countries make different choices to safeguard our common future.

X Appendix

X.I Extinction Condition

To derive the condition in equation (4), it is useful to employ the hypothetical line $\bar{H}$. This line is tangent to $G(S)$, which implies that $\bar{H}'(S) = G'(S)$. It also represents a steady state, so it must satisfy $\bar{H}(S) = G(S)$. After canceling S from both sides of this steady state requirement and rearranging, we find it requires $r(1 - S/K)(S/M - 1) - \alpha\beta L\varphi = 0$. This is a quadratic equation in S, which typically has two solutions as shown by the intersection points A and B in Figure 5. However, when the harvest function is steeper and tangent to $G(S)$, it has only one solution which can be solved for (via the quadratic formula) to find $S = \frac{K+M}{2}$. By substituting this value of S into $\bar{H}'(S) = G'(S)$, and rearranging using the definition of v, we obtain the condition for extinction in the text.

X.II Concentrated and Diffuse Demand

We start from a situation where a fraction β of income is spent uniformly on the unit interval of harvested species. Graphically, the share of income spent on these species is given by the area of the slanted hatched portion in Figure 22. This area is simply β, and the density of demand at any species, which is the vertical distance from the top of this hatched box to the horizontal axis, is also β.

Under the diffuse demand assumption and a set of extinct species given by $[0, \bar{z}]$, the total expenditure spent on remaining species is equal to $\beta[1 - \bar{z}]$. The fraction of income $\beta\bar{z}$ that was formerly spent on harvested species is now reallocated to manufacturing expenditure. The remaining fraction of income spent on harvested species equals the now smaller area of the slanted hatched box to the right of $\bar{z}$ in the figure. Notice the density of demand for those species still in existence - the vertical height to the top of the slanted hatched box - remains at β. This captures the idea that demand is reallocated to other sectors as extinctions occur.

Under the concentrated demand assumption, extinctions occur but demand is now reallocated to those species remaining. It means the density of demand for those remaining over the interval $[\bar{z}, 1]$ rises to $\beta/[1 - \bar{z}]$ as shown in the figure by the vertical line hatched box. Note that the total expenditure on harvested species still in existence - the area of this taller box - is $(\beta/(1 - \bar{z}))(1 - \bar{z}) = \beta$, the fraction of income spent on harvested species we started with. Therefore, this concentrated demand assumption captures the idea that demand is reallocated across the harvested species as extinctions occur.
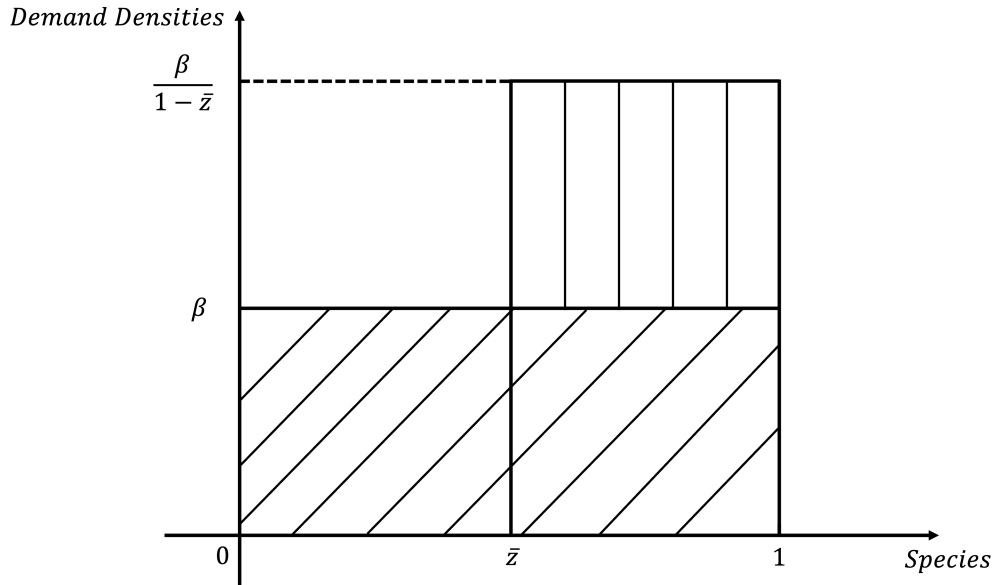
Figure 22: Concentrated or Diffuse Demand

X.III   Simulation Details

The Python code for the simulations is available at https://www.mstaylor1.org/whats-new. The model simulates population dynamics for a system of 12 differential equations. Each of these differential equations has the following general form: $dS/dt = G(S) - H(S)/N$ where $G(S)$ is given by (2) and $H(S)$ by (1). $G(S)$ differs across the species only in the value of r given to it as described below. N divides the total demand for the harvest good uniformly across the finite number of species N. Under the diffuse demand assumption and no habitat loss, the differential equations are independent of each other. N is a constant in this scenario. Under the concentrated demand assumption, the harvest functions are linked because N falls by 1 whenever a species goes extinct. When there is active habitat loss, all differential equations are again linked since their carrying capacity adjusts based on a common change in K discussed below. The time span of the simulation is from 0 to 400, divided into 6000 intervals. The initial population for all species is 1, and the intrinsic growth rates (r), which differ across species, range from 0.2 via increments of 0.035 to 0.6 (excluding 0.6). The carrying capacity K is initially set to 1 and is constant when the habitat is intact. When there is active habitat loss, carrying capacity varies over time according to the simple differential equation $dK/dt = g(M - K)$ where M is the minimum viable population of 0.7. We consider a species extinct when its population falls to 1/1000 of its minimum population value rather than zero. Note a species is destined for extinction whenever its population

falls below M. Other parameters that do not vary across simulations are $\alpha = .7$, $\beta = .5$, $L = 3$, $g = 0.001$, and $\varphi = 1$. Finally, the initial number of species, N is set by the number of possible values of the intrinsic growth rate but falls over time if and when, there are extinctions as defined by the condition above. The interested reader can check that in our baseline case with diffuse demand and no habitat loss, the finite species version of condition (4) is met by only the two slowest-growing species. As noted in the text, to separate the time series for each population it proves useful to measure the harvest product not in terms of population numbers but mass of the harvest. Since size is often negatively correlated with natural growth rates (r), we weigh the harvesting $H(S)$ by dividing by $(1 + 2r^4)$. This scales up slow-growing species and scales down fast-growing species for graphing purposes. It has no bearing on the results.

X.IV   Data Description

X.IV.1   World Capture of Sharks

For the **world production** (i.e., the supply) of sharks we use FAO (2023b), i.e., the updated (version 2023.1.2) "FAO Global Fishery and Aquaculture Production Statistics. Global Capture Production 1950-2021" data (FishStatJ) downloaded from the Food and Agriculture Organization (FAO) of the United Nations in October 2023. We use the time series for ASFIS species and then specify individual shark species and shark groups. See www.fao.org/fishery/statistics/software/fishstatj/en.

This is how we defined the different shark groups in Figure 10 from the "Global Capture Production (1950-2021)" statistics:

All Sharks: We select all "fish, crustaceans and molluscs etc." (a Yearbook/SOFIA subgroup) that have "shark" in the name and exclude live sharksucker and sharktooth moray (which do not belong to the ISSCAAP group "Sharks, rays, chimaeras" and thus are not considered to be sharks by the FAO). We then add shark species which do not have "shark" in their name, but are included in the FAO dataset: Bigeye Thresher, Blackspotted Smoothhound, Bonnethead, Brown Smoothhound, Creek Whaler, Dusky Smoothhound, Great Hammerhead, Longfin Mako, Narrownose Smoothhound, Nursehound, Pelagic Thresher, Porbeagle, Scalloped Hammerhead, Scoophead, Shortfin Mako, Sicklefin Smoothhound, Slender Smoothhound, Smalleye Hammerhead, Smalltooth Sand Tiger, Smooth Hammerhead, Smoothhound, Smoothhounds nei, Spotted Estuary Smoothhound, Spotted Wobbegong, Starry Smoothhound and Thresher. Note that with this definition we slightly overestimate

the true capture of sharks as the relatively large category "sharks, rays, skates etc. nei" also includes rays and skates nei. We prefer this definition to the alternative option of disregarding this group completely as this would imply that, as we found out, a leading large shark-hunting country such as India would not be included in the data; India seems to report her complete capture of sharks only in this non-specific large group of "sharks, rays, skates etc. nei". This, however, further implies that the *level*—not necessarily the dynamics—of the series of the capture data for shark *species* are likely to be too low.

Requiem Sharks: We include all Requiem Sharks available in the FAO dataset except of the Blue Shark and the Silky Shark which are relatively abundant and thus separately shown in Figure 10. Thus, we include the Atlantic Sharpnose Shark, Bignose Shark, Blacknose Shark, Blackspot Shark, Blacktip Reef Shark, Blacktip Shark, Brazilian Sharpnose Shark, Bull Shark, Caribbean Reef Shark, Caribbean Sharpnose Shark, Copper Shark, Creek Whaler, Dusky Shark, Finetooth Shark, Grey Reef Shark, Lemon Shark, Milk Shark, Night Shark, Oceanic Whitetip Shark, Pigeye Shark, Sandbar Shark, Silvertip Shark, Sliteye Shark, Smalltail Shark, Spinner Shark, Spottail Shark, Tiger Shark, Whitecheek Shark, Whitenose Shark, Whitetip Reef Shark and Requiem Sharks nei.

Hammerhead Sharks: We include all categories of Hammerhead Sharks available in the FAO dataset, i.e., Bonnethead, Great Hammerhead, Scalloped Hammerhead, Scoophead, Smalleye Hammerhead, Smooth Hammerhead, Hammerhead Sharks nei and Hammerhead Sharks, etc. nei.

Thresher Sharks: We include all categories of Thresher Sharks availabe in the FAO dataset, i.e., Bigeye Thresher, Pelagic Thresher, Thresher and Thresher Sharks nei.

X.IV.2   World Imports of Shark Fins

For the **imports of shark fins** we use FAO (2023*a*), i.e., the updated (version 2023.1.0) "FAO Global Aquatic Trade Statistics. Global Aquatic Trade–All Partners aggregated–Quantity (1976-2021)" data (FishStatJ), downloaded from the Food and Agriculture Organization (FAO) of the United Nations in October 2023. We use the time series for all shark fins in tonnes (dried, unsalted; fresh or chilled; frozen; prepared or preserved; salted and in brine; smoked, dried). See www.fao.org/fishery/statistics/software/fishstatj/en.

We report the largest shark-fin importing economies and aggregate "China, Hongkong SAR" and China into one group as there is a considerable exchange between them for shark fins. The Rest of Far East and South East Asia (RoFESEA) is composed of Brueni Darussalam, Cambodia, Indonesia, Japan, Myanmar, Philippines, Republic of Korea and Thailand.

The Rest of the World (RoW) includes all other countries available in the FAO data set.

All the time series used in Figure 9 are taken from the FAO data set for the mentioned individual or groups of countries, except for China (including Hongkong) for which we corrected for re-exports of Hongkong and some change in reporting by China. This is how we put together the time series, given that China, Hongkong SAR reports relatively large re-exports mainly destined for China, which in turn, at least for some years, not consistently reports these imports (see Dent and Clarke (2015)):

(1) 1976-1991: we use imports by China, Hongkong SAR as China reports 0 imports; (2) 1992-1994: we use imports by China, Hongkong SAR, deduct its re-exports and add imports by China; (3) 1995: we use imports by China, Hongkong SAR as China reports 0 imports; (4) 1996-2008: we use imports by China, Hongkong SAR, deduct its re-exports and add imports by China; (5) 2009-2016: we use imports by China, Hongkong SAR as China reports unreasonably low imports; 2017-2021: as China, Hongkong SAR reports its "re-exports" as "exports" as of 2017, we use imports by China, Hongkong SAR, deduct its exports and add imports by China. For the most recent years (2020, 2021), the difference between our corrected data and just adding imports of China, Hongkong SAR and imports of China is negligible.

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