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What Have We Learned from the Land Sparing-sharing Model?

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Abstract: The land sparing-sharing model provides a powerful heuristic and analytical framework for understanding the potential of agricultural landscapes to support wild species. However, its conceptual and analytical strengths and limitations remain widely contested or misunderstood. Here, I review what inferences can and cannot be derived from the framework, and discuss eight specific points of contention and confusion. The land sparing-sharing framework is underpinned by an ethic that seeks to minimise harm to non-human species. It is used to quantify how good farmland is for different species, in relation to appropriate reference land uses, and at what opportunity cost. The results of empirical studies that have used the model indicate that most species will have larger populations if food is produced on as small an area as possible, while sparing as large an area of native vegetation as possible. The potential benefits of land sharing or intermediate strategies for wild species are more limited. I review disagreements about the scope of analysis (food production cf. food security), the value of high-yield farmland for wildlife, the (ir)relevance of the Borlaug hypothesis, scale and heterogeneity, fostering human connections to nature, the prospects for land sparing in heavily-modified landscapes, the role of land sparing in improving connectivity, and the political implications of the model. Interpreted alongside insights from social, political and economic studies, the model can help us to understand how decisions about land-use will affect the persistence of wild species populations into the future.

Keywords: biodiversity conservation; agricultural intensification; farmland expansion; wildlife-friendly farming; habitat restoration; trade-offs

1. Introduction

The land sparing-sharing framework originated as a model for quantifying and understanding the implications for wild species of using land in different ways to produce food [1]. It is based on the idea that there are two main ways to reduce the impacts of farming on wild species—making farmland itself more wildlife-friendly, or making more space for unfarmed habitats—and on the observation that there is a tension between these two sorts of interventions. There is a limit to how friendly one can make farmland for wild species without reducing yields, and lower yields mean that more land is needed to produce each tonne of food, making it harder to create more space for nature. The land sparing-sharing model ("the model") provides a framework for researchers to collect and analyse data to understand to what extent this tension exists in the real world, and to estimate how large populations of species would be under land sparing, land sharing, or intermediate scenarios.

Since the publication of the model in 2005, it has been applied to field data from Ghana, India, Uganda, Mexico, Brazil, Uruguay, Kazakhstan and Colombia [2–7]. These empirical, place-based papers, however, have been outnumbered by reviews and other conceptual papers, some positive, but many of them critical of the framework [8–26]. Some have suggested abandoning the framework entirely. I believe that these critiques were written in good faith, and motivated by a genuine desire to correct what the authors perceived as deficiencies of the model. Some criticisms have helped to clarify where further work is needed, and to ensure that issues of social justice and food security, for example, are widely discussed. However, many of the criticisms of the model are misplaced, and the discussion has become unnecessarily polarised. To move from antagonism towards better conversations about conservation and farming, it seems worthwhile to explore these points of misunderstanding. As with other contentious issues, developing a shared understanding of concepts, methods and perspectives is important for constructive interactions [27].

Here, I review definitions of land sparing and related concepts. I summarise what the model does, what it does not do, and what has been learned so far from empirical studies. I discuss the ethical underpinnings of the model, and explore eight contested issues. I conclude that the value and relevance of the model depends on interpreting it appropriately, alongside insights from other disciplines.

1.1. Definitions and Related Concepts

One of the most frequent problems in the discussion is that the term "land sparing" is understood by different people in different ways, and is sometimes confounded with the Borlaug hypothesis, forest transition, sustainable intensification or even eco-modernism. In fact, each of these terms describes something different, and distinguishing between them is crucial for engaging in a meaningful conversation about land sparing and land sharing. I outline here my understanding of these and other terms, the most important of which are defined in Table 1. The land sparing-sharing framework was developed to inform conservation actions, and thus both land sparing and land sharing describe broad categories of what conservation interventions might seek to do.

"Land sparing" is a compound noun, with "sparing" as the gerund. It is thus grammatically equivalent to "thought provoking" or "bird watching" and can also be used as an adjective, as in "land-sparing strategies". It refers to the outcome of intentional conservation interventions that combine increasing yields on farmed land with sparing native vegetation or freeing up land for habitat restoration elsewhere. If land is not spared for nature, then it is not land sparing. "Land sharing" is also a compound noun, and refers to the outcome of intentional conservation interventions that enhance the value of farmlands for wild species. Wild species are those who are not cultivated or domesticated. Land sharing implies purposeful efforts to make farmlands more wildlife-friendly than they would otherwise be. Land sparing and sharing are often abbreviated to simply "sparing" and "sharing".

Land sparing is sometimes conflated with the Borlaug hypothesis [9,23,28–30], attributed to plant scientist Norman Borlaug [31]. Borlaug [32] wrote "that by producing more food per unit of cultivated area more land would be available for other uses, including recreation and wildlife." Land sparing thus refers to a situation where food is produced using higher yields on a smaller area and native vegetation is conserved, while the Borlaug hypothesis posits one way of achieving that outcome: that yield increases will result in what has been termed "passive" land sparing [33]. Yield increases that result in land being spared are also often referred to as "land saving" [28,34]. Evidence for and against the Borlaug hypotheses is reviewed in Section 2.3.

Each of the terms sustainable intensification, ecological intensification and agroecological intensification refer to actions to increase agricultural yields while reducing environmental harm, but each has a distinct meaning [35]. Sustainable intensification refers to actions to "increase food production from existing farmland in ways that place far less pressure on the environment and that do not undermine our capacity to continue producing food in the future" [36]. The focus is on reducing the environmental impacts of food production. Whereas a land-sparing approach situates higher yields as part of the solution for sparing more land for nature, and could be implemented in the context of declining, stable or increasing food production, sustainable intensification situates higher yields as part of the solution for increasing the global food supply, and is usually associated with the imperative to produce more but in ways that are less harmful to the environment [37].

Ecological intensification refers to actions that replace anthropogenic inputs or increase yields by harnessing ecosystem services [38]. Agroecological intensification builds on ecological intensification, with an emphasis on local knowledge and empowerment of smallholders [39]. It is often linked with calls for food sovereignty—for local people to control how food is produced and distributed [40].

Table 1. Some key terms and concepts in the land sparing-sharing literature, together with other terms sometimes used as synonyms, with examples of literature that has used them in that way. Inconsistent use of terms is a source of disagreement. Definitions are condensed from [19,35,36,38,41].

Term	Definition	Terms Used as Synonyms
Land sparing	Increasing yields on farmed land while at the same time protecting native vegetation or freeing up land for habitat restoration elsewhere	Nature sparing [20]
Borlaug hypothesis	The expectation that higher crop yields will result in land being spared for nature	Land saving [34,42–44]; land sparing [20,23,28,30]; passive land sparing [33]
Land sharing	Producing both food and wildlife in the same parts of the landscape by maintaining or restoring the conservation value of the farmed land itself	Wildlife-friendly farming [1,8,10]
Sustainable intensification	Actions to increase food production from existing farmland in ways that reduce environmental impacts and conserve resources	Considerable overlap and lack of consensus in use of these three terms [35]
Ecological intensification	Actions to replace anthropogenic inputs or increase yields by harnessing ecosystem services	
Agroecological intensification	Actions to improve the performance of (typically smallholder) farming systems by using ecological and local knowledge	
Food production	The amount of food produced in a region, not to be confused with yield (production per unit area)	
Food security	Situation where people have physical, social and economic access to sufficient, safe and nutritious food (often conceptualised as availability, access and utilisation)	
Food sovereignty	A community's right to decide how food is produced, distributed and consumed	

The idea of a forest transition has been linked to the concept of land sparing [9]. It refers to the observation that in many countries, forest cover first declines and later increases alongside economic development [45]. The causes of forest transitions are not restricted to the agricultural sector, but include industrialisation and urbanisation. While the occurrence of forest transitions might appear to offer some hope for reconciling conservation and economic development, there are two important caveats. First, most of the "new" forests in the later stages of the transition are plantations, secondary forests or managed forests, which typically have lower value for biodiversity than primary forests [46]. Second, a focus on national-level patterns ignores international trade. Wealthier countries may experience a forest transition while outsourcing their demand for wood, food and other land-demanding products to other countries [47]. Evidence for forest transitions is thus not evidence that overall, land has been spared for nature.

Land sparing has been associated with ecomodernism [48], an environmental philosophy which argues that to save nature, humanity must use technology to decouple human development from environmental impact [49]. But while Phalan et al. [10] described land sparing as a way to minimise the inevitable harm of food production, ecomodernists are more positive, and view decoupling as a pathway towards a "good Anthropocene". Those using the land sparing-sharing framework see reductions in consumption as an important part of the solution [2,7,50], whereas ecomodernists do not. Those using the sparing-sharing framework are agnostic about how yields should be increased, and welcome initiatives involving farmer knowledge networks and ecological intensification; ecomodernists focus almost exclusively on modern, technological solutions [51].

To summarise, land sparing and land sharing describe two ends of a continuum of intentional spatial organisation of food production and biodiversity conservation: whether separated or integrated. The Borlaug hypothesis describes one possible way in which land sparing might be achieved:

as a consequence of increasing yields. Forest transitions describe increases in countries' forest cover as a consequence of economic development, but they do not necessarily ensure that land is spared for nature. Ecomodernism is a philosophical stance adopted by some technological optimists and humanists. Sustainable intensification, ecological intensification and agroecological intensification refer to methods for increasing yields while reducing the environmental impacts of farming, and may or may not incorporate some land sparing and/or sharing.

1.2. What Does the Model Do?

The land sparing-sharing model provides an analytical framework for asking questions about the value of agricultural land for wild species. The model requires data on the densities of wild species across a gradient of agricultural yields, from unfarmed land to high-yielding farmland. Density–yield curves are fitted to the data, and are used to project the population-level outcomes of different combinations of land use that meet a series of specified production levels. The model is described in detail elsewhere [1,2]. Here, I describe its conceptual advantages over previous methods. Some forms of agricultural land management, such as agroforestry or organic farming, are commonly described as being "good for biodiversity". The model, in simple terms, helps to clarify:

(1) *how good* they are,
(2) for *what species*,
(3) in relation to *what reference*, and
(4) at *what cost*.

Understanding how good farmed landscapes are for wild species is important, because suitability varies on a continuous, not binary, scale. The land sparing-sharing model made an important advance on previous work by using the population density of each individual species as a metric for habitat quality. Previously, the most common metric used in the literature was sample- or site-scale species richness [52,53]. Biodiversity, however, is much more than species richness. Although species richness continues to be used, it is rarely, if ever, an appropriate focus for land managers, because it fails to detect changes in species composition (for example, the replacement of restricted-range species and grassland specialists by widespread generalists) and is blind to changes in population size (a species can decline by 99% at a site and still count towards richness) [54,55]. Commonly-used diversity indices, such as Shannon richness, have similar weaknesses.

Analysing how population densities of each species respond to land conversion and yield increases allows us to identify which species are negatively affected by agriculture, and which species benefit from it. If we assume that humans have an equal responsibility to each species not to eliminate it, then we should focus most attention and resources on those in greatest danger of extinction. By analysing population outcomes for each species separately, the land sparing-sharing framework enables researchers to identify which species are harmed and which benefit from farming, and to understand effects on species which are already threatened or which have restricted ranges.

Studies purporting to show "high" biodiversity or "high" yields within an agricultural system must define "high" in relation to some reference. If we are interested in the impacts of agriculture, then the appropriate reference for population density is that in unfarmed native vegetation. For yields, it is the maximum attainable yield that can be sustained in the long term. The land sparing-sharing framework provides a way to incorporate both of these reference states.

Finally, all conservation comes at a cost. One of the main costs in an agricultural context is opportunity cost: food not produced because land is kept uncultivated or farmed using lower-yield methods [56]. The particular relevance of opportunity cost for land sparing and land sharing is that if yields are reduced in one place, some of the forgone production is likely to be displaced (and have impacts on biodiversity) elsewhere. This effect is illustrated by yield reductions caused by crop diseases, which have prompted greater reliance on imports [57]. Assessments of the outcomes of wildlife-friendly farming or protected areas have often overlooked this leakage problem by ignoring the land-sparing potential of higher-yield farming. While the land sparing-sharing framework is a model of biophysical, not economic, relationships, and is not designed to predict land-use change, it provides an approximate way to measure opportunity cost and internalise leakage. The implicit assumption is that displacement of food production elsewhere would result in the same amount of harm to biodiversity as if it were retained within the focal landscape.

1.3. What Does the Model Not Do?

A good way to think about the land sparing-sharing model is that it is intersectional (distinct but overlapping) with other questions about food, land use and conservation. There are many such questions, and the model does not address all, or even most, of them. Like all models, this one provides a partial and simplified view of reality. Like all models, its purpose is not to provide a complete description of the world, but to provide useful information about a specific question. Using density–yield curves to understand how species respond to agriculture can be conceptualised as one part of a metaphorical elephant (Figure 1). We can put what we learn from the model together with what we learn by asking other questions, as we search for answers as to how to reconcile human demand for food, and conservation.

To give an example, the model does not address the social organisation of farming. Among the complex web of factors that have driven smallholder farmers into poverty traps are trade liberalisation, unequal access to land and capital, and development policies focused on commercial export crops [58]. Meanwhile, the results of land sparing-sharing studies indicate that protecting as much native vegetation as possible, even if that means higher-yield farming, is likely to be the best way to conserve wild species (see Section 1.4). Are these two findings in conflict? No. We must take both into account if conservation and human development are to succeed. Taken together, what they imply is a need to spare land for nature while at the same time supporting policies that level the playing field for smallholders. How to do so will depend on local circumstances [59], but could involve strengthening land rights and other institutions, making it easier for smallholders to access and share information, technology and resources to increase yields and restore habitats, and funding research into agronomic and agroecological methods appropriate to the local context.

The original formulation of the land sparing-sharing framework omits some complexities, but it can be and already has been modified to incorporate many of these, including spatial configuration and the influence of edge effects [60,61]; the influence of changing diets and reducing food waste [50]; inclusion of some ecosystem services [4,7,50,62]; prediction of the effects of specific public policies [63]; and application to forestry [64,65], urban planning [66–69] and marine conservation [70]. It is a model, and so all assumptions can be varied and tested. Further modifications have been suggested to incorporate species dispersal and source-sink dynamics [71], heterogeneity at multiple scales [15,22], analysis of outcomes for food security and human wellbeing [72], use of optimisation techniques and more complex mixes of land use [73] and replacement of imprecise terms such as "win-wins" with more clearly-defined concepts such as Pareto improvement [74]. An important challenge is to move beyond vote-counting towards developing conservation plans that ensure populations of all species in a region are sustained.

Figure 1. The land sparing-sharing model can be conceptualised as one part of a metaphorical elephant. Each blind man (representing different areas of research) has access to part of the truth, but his knowledge is of limited use until combined with that of the other blind men. Similarly, the land sparing-sharing model provides useful information on how species respond to land conversion and yield increases, but this knowledge is of greatest use for decision-making when it is combined with other information, for example from economics, behavioural psychology and political ecology. Image: Blind monks examining an elephant, by Hanabusa Itchō (1652–1724). Public domain.

The land sparing-sharing model has been criticised for "ignoring" politics, rural livelihoods and governance [11,75]. This criticism reflects a misunderstanding of the purpose of the model. Just as climate models serve to predict the effects on global and regional climate of adding certain amounts of greenhouse gases to atmosphere, the land sparing-sharing model serves to predict the effects on wild species of using land in different ways to produce food. And just as social, economic and political factors will determine what action is taken to limit climate change, similar factors will determine what action is taken to limit the impacts of land-use change and food production on biodiversity. Predictions of global climate forcing are apolitical, and yet the insights they provide are essential for informed advocacy and activism. Similarly, an accurate quantitative understanding of how land-use decisions affect wild species is an essential starting point for informed conservation action. If our aims are climate justice and just conservation [76], we must integrate model insights with social and political knowledge as we strive towards both social and inter-species justice [77,78].

1.4. What Have We Learned So Far?

A relatively small number of empirical studies have collected all of the data necessary to apply the land sparing-sharing model. Many other empirical and theoretical studies have referenced the concepts [26], but have failed to include data on an unfarmed baseline, to measure the densities of large numbers of individual species, to quantify farm yields, or to calculate the total population effects of different land-use choices [10,19]. Those other studies can sometimes provide useful information. However, any conclusions they draw about the merits of sparing and sharing from the shape of curves with species richness on the *Y* axis, for example, are unreliable. Here, I focus on what we have learned from studies that used the land sparing-sharing model proposed by Green et al. [1], or which modified it [4,7] while adhering to the critical points mentioned above.

The key finding from all empirical studies to date, covering >1500 species, is that most species would have larger populations if a given amount of food is produced on as small an area as possible, while sparing as large an area of native vegetation as possible. This is true for birds and trees in the Upper Guinea forests of Ghana [2], birds and trees in the Upper Gangetic Plain of India [2], birds in Uganda's banana-coffee arc [3], birds and dung beetles in the Colombian Chocó-Andes [4], birds in the Kazakhstan steppe [5], birds in the Pampas grasslands of Brazil and Uruguay [6], and birds, trees and dung beetles in the Yucatán, Mexico [7]. It is especially true for species with small global ranges, which are often those of most conservation concern. The majority of species—specialists and generalists alike—are negatively affected when their habitats are converted to agricultural use, even to apparently benign uses such as diverse landscape mosaics with agroforestry plots and fallows. A typical example is the Chocolate-backed Kingfisher *Halcyon badia* (Figure 2), for which even the most complex agroforests offer a poor substitute for its native forest habitat. A few species benefit from conversion, including some not found in the original native vegetation types. So, the species in most need of help are those who would be most favoured by land sparing, while land sharing is of little benefit to such species.

Figure 2. Chocolate-backed Kingfisher (*Halcyon badia*). As is typical of many forest resident birds in southwest Ghana, this species is absent from farm-fallow-agroforestry mosaics (Photo: L. Holbech).

Why might we see such consistent responses across taxa, continents and biomes? One part of the reason is that most species are relatively specialised and rare [79]. We might expect that the habitat structure and resources they depend on are easily disrupted, even by relatively subtle changes such as understorey clearance to grow coffee or cocoa. Farming eliminates niches by diverting land, water, light and nutrients for human consumption [80]. Adopting more benign methods may not help much; at the same yields, organic farming is no better for invertebrate diversity than conventional farming [81]. It is not that wildlife-friendly farming systems fail to provide habitat for many species—they do [82]. But they fail to provide good quality habitat for most of the species that would occur in the absence of farming.

There are some interesting nuances to these results. The farming systems with most conservation value, such as lightly-grazed semi-natural grasslands, are so low-yielding as to make little meaningful contribution to food supply [5,6]. Although some species peak in density at low or intermediate yields—in high-nature-value farmland, as it is termed in Europe [83]—they do so in farmland with yields too low to maintain current food production if scaled up. Such systems are often also uneconomic, even with subsidies, and are prone to abandonment or intensification [84,85]. If we wish to preserve these systems, we are better to do so primarily for their ecological and cultural values, rather than positioning them as a model of production and conservation in harmony. This could be supported by reforms to agricultural and agri-environmental subsidies [86]. Sparing of low-yield farmland necessarily competes with the sparing of unfarmed land, and may require yields to be increased elsewhere [6]. The sparing-sharing model can be readily adapted to examine the sparing of high-nature-value farmland alongside native vegetation, using mixed scenarios with multiple compartments rather than two as in the original model [73,87].

Although such mixed scenarios merit further investigation, the results of sparing-sharing studies indicate that wildlife-friendly farming has serious limitations for conservation. Narratives proposing that countryside habitats offer a "win-win" for people and nature are appealing. However, such narratives have often relied on species richness to measure biodiversity, have failed to test any alternative configurations of land use, have omitted reference systems, or have not specified what evidence it would take to show that countryside habitats offer a poor deal for wild species [10]. Instead, the data collected so far suggest that protecting and restoring as much native vegetation as possible would be more beneficial for wild species than making farmlands more wildlife-friendly. The data show that even the most wildlife-friendly systems are missing many species from the native ecosystem, and that most of these farming systems are low-yielding.

How should these findings be used by decision-makers? They help to clarify that what wild species need, much more than they need wildlife-friendly farming, is large areas of native vegetation. This insight does not exclude the possibility that decision-makers might prefer intermediate strategies for social or political reasons, or for conserving certain species, but they clarify that such strategies represent a poor compromise overall for biodiversity conservation. The findings do not imply that land sparing will be optimal for other objectives too, such as ecosystem service provision or food security. It may (or may not) be that more complex strategies are optimal when other objectives are included. Some objectives can be readily combined on the same land, while others cannot. What is clear—at least in the growing set of places studied so far—is that separation of food production and conservation on different areas of land, rather than integration, would be the most effective way of reconciling these two objectives.

This tells us something useful about how conservation efforts might be focused. In Ghana, for example, actions to prevent any further forest loss and degradation in forest reserves are likely to be more beneficial for biodiversity than promoting wildlife-friendly cocoa agroforestry. In Kazakhstan, concentrating food production on existing croplands will cause less harm to biodiversity than converting intact and grazed steppes. The land sparing-sharing model is best thought of as an aid to understanding the technical potential of different modes of agriculture to support wild species. It cannot predict land-use change, but can be used as a tool for predicting the consequences of land-use change for species populations. As one part of an elephant, information on density–yield responses should be integrated with social, political and other information when making decisions.

1.5. Choices about Farming and Land-Use Are Underpinned by Ethics

The land sparing-sharing model was developed with the implicit recognition that non-human species have their own intrinsic value, independent of any contribution they make to human wellbeing. Its aim is to identify how to meet human needs (in this case, food production) with least harm to non-human organisms. There is increasing recognition that humans have various ethical responsibilities towards other species, not least an obligation not to eliminate them [78,88,89]. The model does not provide information on how to weight the objectives of producing more food or conserving species populations, and it does not attempt to combine them into a single objective function. While the model could be adapted to trade off one anthropocentric objective against another [24], that is not its original purpose, and in my view, it would be a mistake to sideline the intrinsic value of wild species.

This emphasis on the intrinsic value of wild species is perhaps one of the most important, yet overlooked, reasons that different authors have come to different conclusions about sparing and sharing [17,38]. Broadly speaking, concern with preventing the disappearance of wild species underpins the logic and analyses of the land sparing-sharing framework: how do we meet a human need at least cost to nonhuman species? Those favouring land sharing tend to gravitate towards a different question: how do we design landscapes that meet a range of human needs? Biodiversity conservation is conceptualised as one small component, and replacement of some species by others is seen as undesirable only to the extent that it undermines human interests. Emphasising the needs of wild species is consistent with an ecocentric ethic, which sees humans as one species among many, and values non-human species for their own sakes [90]. A risk with ecocentrism is that by seeing humans as a single species, we may overlook injustice between different groups of people [91]. Focusing on human wellbeing is more consistent with an anthropocentric ethic, where non-human species have value only in relation to humanity [92], and where "biodiversity" is used to refer primarily to the diversity of crops, livestock and farmland [93]. A risk with anthropocentrism is that by focusing on human wellbeing, we may ignore the needs of species who are not useful or valuable to us. Attention to both the needs of vulnerable groups of people, and to those of non-human species, is needed if we are to pursue "just conservation" [76].

The sparing-sharing model places most emphasis on understanding what wild species need, given the constraint of food production for humans. It is thus informed primarily by an ecocentric ethic, but this should in no way preclude additional consideration of social justice and nature's contributions to people too [94]. Better understanding of one part of the elephant should be seen as complementary, not competitive, with understanding other parts of the elephant.

Nevertheless, conserving farmland biodiversity for the services it provides (ecological intensification) is not the same as conserving on-farm biodiversity for its own sake (land sharing). Ecosystem services from on-farm biodiversity can contribute to food production, and can in many cases support sustainable increases in yields [38]. However, actions to promote service-providing biodiversity are insufficient to conserve those species that have little direct service value [95]. Such species—probably the majority of life on Earth—will benefit if humanity can produce the same amount of food on less land (including through ecological intensification), while conserving and restoring native vegetation elsewhere.

2. Points of Contention, Confusion or Concern

2.1. A Model of Food Production, Not Food Security

The sparing-sharing model was developed in recognition that agriculture, of all human activities, poses the greatest threat to wild species [1]. The focus of those using the model is to understand how to conserve biodiversity in the face of the twin threats of agricultural expansion and intensification. Both habitat loss (for any sort of farming) and "intensive" farming (whether measured in terms of inputs or yields) change nature. When these changes include population declines or extirpations, and thus reduce the chances of species persisting into the future, we can consider them harmful to biodiversity. The model addresses one crucial question which is needed to inform conservation efforts: what effect would different ways of producing the same amount of food have on populations of wild species?

This framing places the use of land for food production centre-stage [17]. Which causes least harm to populations of wild species: agricultural expansion, intensification or some intermediate combination of the two? Comparisons are made per unit of food produced. Critics of the framework point out, correctly, that food production is not equivalent to human wellbeing. And, while it cannot be dismissed [96], increasing food production is not the main thing needed to address food security [14,17,97]. We can also note that making farmlands more hospitable to wildlife is not the main thing needed to address food security. Human use of land to produce food is, however, the main constraint limiting habitat availability and quality for many wild species.

Observations that food production is increasing and projected to continue doing so [98] are something conservationists worry about, not cheer on. The land sparing-sharing framework does not assume increases in food production (a point often misunderstood, when production is confused with yields). Rather, it compares higher-yield farming on less land, with incrementally lower-yield farming on more land. It enables these comparisons for scenarios providing the same amount of food as at present, for scenarios of increased food production, and for scenarios with reduced food production. It is not hard to imagine a shifting cultivation landscape providing higher food security than a biofuel plantation, where only the former produces food that people eat. However, it is also not hard to imagine a scenario in which high-yield, permanent cropping produces more food and better food security outcomes than either shifting cultivation or biofuel plantations, and is compatible with sparing more land for nature.

Understanding the biophysical question of how to produce a given amount of food with least impact on wild species is important as we seek to define better food systems. Assuming that particular production methods have inevitable food security outcomes leaves us stuck within the paradigms of the present. To assume that agroecological farming methods—for example—feed more people than other methods regardless of whether they are high-yielding, is to assume that it is impossible to co-opt other high-yielding farming methods to improve food security rather than increase corporate profits. Instead, we can imagine a future in which, for example, smallholder farmers have access to the knowledge and technology that enables them to produce yields as high as those currently produced by large-scale producers. Food security and biodiversity conservation are intersectional issues, each with their own sets of necessary solutions, which do not always align but neither do they inevitably conflict. If, in a certain region, what non-human species need is more, better-quality habitat, and what humans facing food insecurity need is greater autonomy alongside regulations that curb the abuse of corporate power, then what those of us concerned with conservation and human wellbeing must do is find ways to deliver all of these things together. It would be a mistake to privilege one set of needs and ignore the other.

Where does this leave the measurement of food security in analyses of conflicts between conservation and food production? Quantifying current food availability, access and utilisation is important in diagnosing human wellbeing in present-day landscapes [41]. Maize yields in the United States, for example, are relatively high, but because so much of the crop is used as animal feed and biofuel, its contribution to food security is much lower than it could be [99]. However, maize is also a staple food crop in many parts of the world, and so its high yields could in principle contribute to feeding many people per hectare. Similarly, high-yield soybean production could in principle produce much nutritious food from a small land area, but feeding the soybeans to livestock first (even with biodiesel as a co-product) consumes more land and contributes less to human wellbeing [99]. Most of the benefit of high-yield soybean production in Brazil has accrued in wealth and political influence to a small group of wealthy landowners [100]. Density–yield analyses using the land sparing-sharing framework can point us towards better ways of configuring land use to meet the needs of both humans and those of wild species, but overcoming the vested interests that will resist changes remains an important social and political challenge.

Perhaps the most useful way forward when considering future scenarios for agriculture is to incorporate a range of assumptions about how food is used, ranging from current production-system-specific patterns to the best case where waste and wasteful uses are avoided, and where the nutritional quality of food is optimised. Maximising the benefits of any strategy on the land sparing-sharing continuum will depend on using food efficiently to feed people. Importantly, these analyses are designed to predict what could happen in a given region, not what will happen.

An example of this sort of analysis is given in Figure 3. Figure 3A shows the plausible option space for reconciling conservation and food production, with its limits set by the efficiency frontier, or production possibility frontier [101]. Producing the same amount of food as at present would, based on what we have learned from empirical studies to date, be better for wild species if done through a land-sparing strategy (SP1) than a land-sharing strategy (SH1). Intermediate strategies are not shown for simplicity, but would likely lie between SP1 and SH1. Sparing would also be best if total food production increases (SP2 and SH2). Note that win-wins (maximising food production while maintaining healthy populations of all species) will typically not be feasible. Figure 3B shows the plausible option space for reconciling conservation and food security in the same region. The efficiency frontier can be shifted to the right by addressing systemic problems such as losses through food waste, and social inequality which restricts access by the poor to sufficient, nutritious food. If land sparing involves high-yielding methods that divert more food to wasteful uses such as biofuels and livestock production (as high-yielding methods in use today often do), then it might feed fewer people even while producing the same amount of food (SP1′). If land sharing produces no more food than at present, but is based on social relations that ensure that those who most need it have access to it, then it might feed more people even while producing the same amount of food (SH1′). However, we can also envisage a land-sparing scenario in which food is used as efficiently as in SH1′ to feed people, while land is used as efficiently as in SP1′ to maximise the area spared for nature (SP1″).

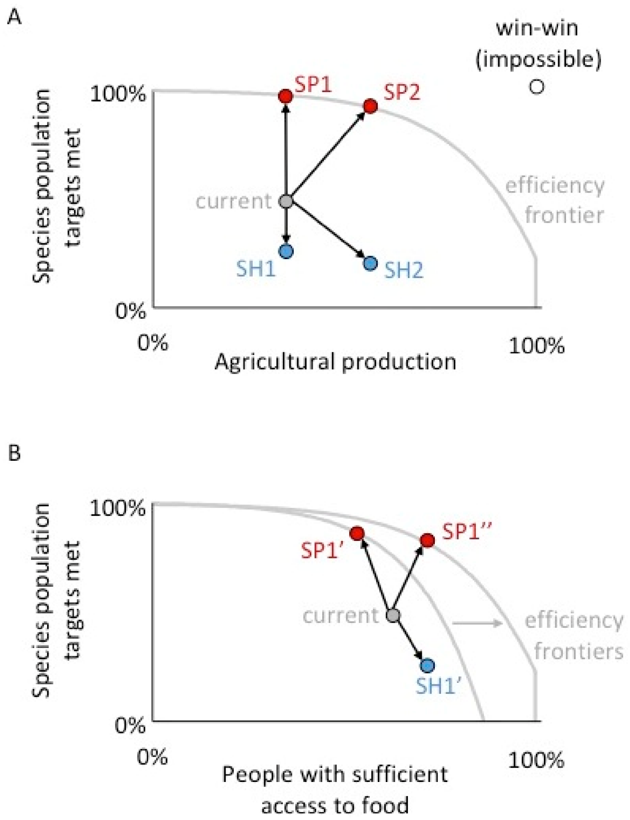

Figure 3. Schematic efficiency frontiers for (**A**) conservation and food production, and (**B**) conservation and food security (access to food) in a hypothetical region. Points show outcomes from current land use in a region (**grey**), land sparing scenarios (**red**) and land sharing scenarios (**blue**). The *X* axis shows (**A**) total agricultural production, scaled relative to the maximum level that could be sustained from the region, and (**B**) the percentage of people with sufficient access to food. The *Y* axis shows the percentage of the original species of the region whose populations are maintained at a desirable level (e.g., with <1% chance of extinction in the next 100 years). For further explanation, see text. In (**B**), the efficiency frontier can be shifted to the right by addressing systemic barriers to food access, such as social inequality, diets and food waste.

2.2. *Is High-Yield Farming Necessarily Devoid of Biodiversity?*

A common assumption in criticisms of the land sparing-sharing framework is that high-yield farming implies the use of "conventional" or "industrial" intensification [12,14]. This assumption is incorrect. The framework is not limited to analysing any one form of farming. In a situation where agroecological methods produce a lot of food per hectare and "conventional" methods produce little food per hectare (as assumed by [14]), then agroecological methods will be those with the greatest potential to contribute to a land-sparing strategy. In addition to more conventional inputs, studies using the model have proposed supported knowledge-intensive smallholder farming [2], traditional snow accumulation techniques [5] and silvopastoral systems [7] to increase yields in a land-sparing context.

High-yield farming need not be "entirely inhospitable to wildlife" [20], nor is wildlife-friendly farming necessarily low-yielding. Farmland yields may be enhanced by the presence of some level of biodiversity to provide services such as pollination and pest control [38,102]. Maintaining some biodiversity in farmlands may also confer resilience to events such as pest outbreaks [103]. The crucial point for conservation, however, is that providing conditions for useful species on farmland is unlikely to be enough to help the majority of species who make little contribution to agricultural productivity [95]. While there are good reasons to expect that high yields will limit the possibilities for conserving non-functional wild species on farmland, the best test of such ideas is through the collection and analysis of field data. That is also the best way to test the assumption that alternative forms of agriculture are necessarily better for wild species. The land sparing-sharing model provides one framework for testing these assumptions. What is useful about the framework is that it provides a clearer way of defining biodiversity (in terms of the population-level responses of individual species) than previous methods.

Overturning these assumptions can help to clarify some points on which critics and proponents of the land sparing-sharing framework agree. Where yields are comparable, farming methods that minimise other negative environmental impacts are to be preferred over methods which involve excessive use of pesticides, fertiliser and irrigation. Both Kremen [20] and Green et al. [1] are in agreement that a "both-and" approach is desirable to the extent that trade-offs can be avoided. Methods for high-yield farming which degrade the soils and water supplies on which production depends cannot form part of a long-term land-sparing strategy. Intensive production practices which do not sustain high yields have no part to play in land sparing. Similarly, the social and political relations of high-yielding systems which contribute little to food security or other aspects of human wellbeing, such as the maize and soybean examples discussed earlier, will need to be dramatically reconfigured if they are to form part of an effective land-sparing strategy. This might seem daunting (it is), but successful conservation will need systemic change at both local and wider scales [104], and requires engagement with radical ideas such as ending governments' focus on economic growth as a policy objective [105], devoting half of the Earth to conservation [78,106,107], and governing land as a global commons [108].

2.3. Will Yield Increases Lead to Land Sparing?

The question of whether yield increases will result in land being spared for nature is often conflated with the question of whether land sparing is a desirable objective. They are two distinct issues, and the sparing-sharing framework addresses only the second. High yields are a condition for land sparing, and not by themselves a particularly effective lever by which to make it happen. Other, more effective levers involve spatial planning, economic incentives, certification, and strategic deployment of infrastructure, knowledge and technology [33,109]. Nevertheless, the Borlaug hypothesis can also play a role in the case of passive land sparing, and so it is worthwhile to summarise the evidence for and against it.

The Borlaug hypothesis—that improvements in agricultural technology will spare land for nature—is often contrasted with the Jevons paradox. William Stanley Jevons noticed in the mid-nineteenth century that as coal-powered engines became more efficient, the total amount of coal used did not decrease, but increased [110]. The Jevons paradox is sometimes treated as synonymous with the rebound effect, but the effect that Jevons described was an extreme form of rebound: a backfire effect. In an agricultural context, rebound effects mean that less land is spared than could be, given the magnitude of yield increases, while backfire effects mean that not only is no land spared, but that more land is converted than would be the case without yield increases. Neither the Borlaug hypothesis nor the Jevons paradox have received strong support from empirical studies [42]. Instead, there is evidence that yield increases usually reduce the rate of land clearance to some extent, but that this land-saving effect is smaller than it could be, because of a rebound effect [34,42,111,112].

The relationships between yield increases and deforestation are complex. Introduction of kudzu (an invasive green manure crop) in the Peruvian Amazon, for example, reduced clearance of primary forest but increased clearance of secondary forest [113]. Improved pasture practices in Latin America tend to be associated with greater deforestation, but this can be avoided if the practices are introduced alongside forest conservation policies [111]. Recipients of agricultural assistance in Malawi reduced extraction of commercial forest products without clearing more land, suggesting that yield increases were associated with reduced pressure on forests [114]. The most detailed exploration of these issues is in an edited volume by Angelsen and Kaimowitz [31], who identified some of the conditions whereby yield-increasing technologies can help to spare land: labour- and capital-intensive technologies, capital-constrained farmers, local output markets, staple crops with low price elasticity of demand, segmented labour markets with limited mobility, and technological improvements in sectors away from the forest frontier [111]. Yield increases which are associated with deforestation at a local scale may be land-saving at national or global scales, suggesting that efforts to increase agricultural yields should be focused away from regions with the highest conservation value.

At country level, cropland area has increased more slowly than agricultural production: there is weak evidence for land savings in developing countries [115] but paired declines in cropland and yield increases have been rare [112]. The land savings achieved because of yield increases during the Green Revolution were far less than predicted by Borlaug [116]: in the region of 20 million hectares rather than 560 million, and of this, only 2 million hectares of forest [34]. The higher yields of the Green Revolution were used primarily to produce more, cheaper food, not to spare land for nature. The overarching conclusion is that the Borlaug effect is weak, unreliable, and may not spare the land of most conservation value. Therefore, targeted environmental policies—centred on land-use zoning [117], forest protection [118] and incentives for conservation and restoration [119]—need to be strengthened to ensure that land is spared [109,120].

The need for land-sparing mechanisms to avoid rebound effects is as pertinent to high-yielding agroecological methods as it is to high-yielding conventional methods. Proponents of alternative agriculture often use land-saving arguments, proposing that by increasing yields, intercropping systems or agroforestry will reduce pressure on forests [121,122]. This may be more likely in situations where those techniques are labour-demanding, generate food for local markets, and do not increase profitability at the forest frontier. But the Borlaug effect is likely to be imperfect even in these cases, and so even where wildlife-friendly farming is high-yielding, finding ways to ensure that land is spared for nature remains crucial for conservation.

Equally (or more) important as the Borlaug effect is to consider the extent to which protecting habitats leads to yield increases—rather than simply displacing agricultural production. Ester Boserup [123] observed that increasing yields is often labour-intensive, and so farmers prefer to expand the area of low-input farming until land becomes scarce, and only then work to increase yields [124]. Boserup emphasised human population increase as the driver of land scarcity, but there is also support from modelling and empirical studies for the idea that protecting native vegetation will prompt increases in agricultural productivity [125,126]. Some displacement, or leakage, may also occur [127], although this effect may be weaker than sometimes feared [128]. The risk of leakage reinforces the need to combine enforcement and incentives for habitat protection and restoration with efforts to increase yields.

2.4. Scale and Heterogeneity

Scale and heterogeneity have been recurrent topics of discussion in the sparing-sharing literature [8,15,22]. Deciding on the appropriate spatial extent and spatial grain size is important for many ecological questions, and the sparing-sharing model is no exception [17]. Extent refers to the entire region or landscape considered in a study, and to which inferences are applied. Grain size refers to the size of sampling units within that region or landscape. It is helpful to define study extents to be as homogeneous in physical characteristics (terrain, climate, soil types) as possible, because this reduces the number of confounding variables that need to be accounted for. Extents might additionally be defined using political (e.g., county or state) boundaries relevant to decision-making.

Grain size can be similarly defined in relation to both ecological and political relevance [10]. Units of land that could be spared or shared should be large relative to the home range of the focal species, and of a size relevant to decision-makers. Various studies have focused on different grain sizes [17,22], and while there are inevitable grey areas, there are two reasons it would be a mistake to refer to the protection of very small features on farms (e.g., field margins, small ponds or isolated trees) as land sparing. First, such interventions are unlikely to provide sufficient habitat on their own to support a viable population of most species. Second, the point of considering scenarios towards the land-sparing end of the sparing-sharing spectrum is to widen the range of options considered. Ideally, land sparing involves safeguarding or restoring blocks of native vegetation that are several square kilometres to several thousand square kilometres in size, in landscapes that are many hundreds of square kilometres to tens of thousands of square kilometres in extent [129]. This scale implies a grain size of the order of 1 km^2, embraces the needs of almost all species, and aligns with the areas over which major land-use decisions are made. Protecting hedgerow trees and other on-farm features can provide some ecological benefit, especially if the opportunity cost is minimal. However, both the ecological benefits and the costs of such actions should be compared with the sparing of very large blocks of land as well.

For land sparing to succeed, it must incorporate the full range of heterogeneity that existed within a landscape prior to farming [15]. Farming on all the fertile soils in a region and "sparing" only land that is rocky and infertile, for example, would fail to protect species associated with fertile soils. Spared land should incorporate a mosaic of successional stages and ecotones, not simply a single climax ecosystem such as closed-canopy forest. Conservation of small features of disproportionate importance, such as desert springs or caves [130], might be incorporated into spared or shared land. There may be trade-offs between sparing areas large enough to protect wide-ranging species and processes, and sufficiently numerous to capture beta diversity: multiple-scale land sparing might help resolve such trade-offs, although it also raises new ones [22].

Temporal scales also merit consideration, although they pose challenges for field data collection [17,20]. It is difficult to measure source-sink dynamics, and over time, species populations in either fragments of vegetation or in shared land may not persist [71]. One response is to collect long-term data. Studies that have done so reinforce the conclusion that only sparing of large blocks of vegetation will be sufficient to stave off extinctions, and provide time for remedial actions such as forest restoration [129]. Trade-offs between sparing, sharing, and intermediate or mixed strategies have not yet been explored in this context, but land sharing seems unlikely to offer greater conservation benefit than the matrix of recovering secondary forests that has been studied. In the meantime, maintaining species populations which are as large as possible seems most likely to maximise their chance of persistence [131].

2.5. Fostering Human Connections to Nature

Concern has been expressed that land sparing could reinforce the separation of humans from nature [132]. Providing opportunities within landscapes for people to connect with nature is an important consideration for decision-makers [10,17]. Contact with nature improves people's wellbeing, their understanding of their environment, and their support for conservation [133,134]. To understand this issue, it is important to realise that land sparing is not about separating human beings from nature; it is about separating agriculture from nature. A case can be made that any strategy along the sparing-sharing continuum would help to improve access to nature, by increasing the probability of finding certain species in the farmed landscape (land sharing) or through providing more, larger, or higher-quality areas of native vegetation that support a multitude of species (land sparing).

Among the most effective ways to improve access to nature could be to develop parks in urban centres [135] and to foster feelings of connection with nature, which are a stronger predictor of time spent in nature than accessibility [136]. A further consideration is that human recreational use can have negative impacts on wild species [137,138]. The sparing-sharing framework explores only the impacts of agricultural land use, but other forms of use such as recreation could be addressed with a modified version of the sparing-sharing framework: what are the consequences of concentrating visitors in a few sites, or parts of sites, versus providing more widespread, dispersed access?

2.6. Land Sparing in Heavily-Modified Landscapes

Some authors have suggested that the sparing-sharing model is irrelevant in regions where little intact native vegetation remains, including temperate regions [13], the Brazilian Atlantic Forest [139], or El Salvador [20,140], and that actions in such regions should focus on land sharing. I disagree that this is a foregone conclusion. As highlighted by others [8,84], habitat restoration is also possible in such landscapes. Forest restoration to enlarge, buffer and reconnect remaining fragments will be needed to prevent more species from sharing the fate of three recently-extinct bird species in the Atlantic Forest [141]. Options along the sparing-sharing spectrum can be considered in any landscape, with any starting point, although the benefits of restoration take some time to accrue [50]. In regions where little native vegetation remains, but where land clearance has occurred mostly in recent decades, restoration may offer the best hope for reducing extinction debt [142], and can also provide ecosystem services, restore cultural value and generate livelihood opportunities [143].

In regions where some species have become entirely reliant on farmed landscapes, and where native megafauna who structured habitats are extinct, the challenges are even greater [144]. Some components of 'traditional' farming might act as surrogates for tamed natural disturbance processes and provide ecological niches for early-successional species [84,145]. Nevertheless, habitat restoration and rewilding could also provide for these species, if developed as part of long-term conservation strategies [86,146]. Perpetuation of land-sharing practices might be desirable in such landscapes, at least in the short term [147], but in the longer term, I advocate considering a wider range of strategies for balancing the needs of humans and other species.

2.7. Climate Change, Range Shifts and Connectivity

One of the most appealing arguments for land sharing is that even if it, in itself, provides only relatively poor habitat, it could reduce isolation between fragments of forest or other remnant vegetation. Many farming methods create barriers to species dispersal, but there are multiple ways to improve connectivity. Land sparing, by increasing the proportion of native vegetation in the landscape, could be as or more effective than intermediate approaches in facilitating animal dispersal [148]. Evidence suggests that larger, high-quality areas of natural habitats can increase functional connectivity, promote colonisation in the face of climate change and habitat fragmentation [149], and buffer species from the effects of climate change [150,151]. Protected areas have been shown to act as 'landing pads' and then 'establishment centres' for species shifting their ranges because of climate change [152].

The key to understanding how best to improve connectivity in agricultural landscapes lies in quantifying the benefits to the most dispersal-limited species, and comparing different solutions at similar levels of cost. Trade-offs between minimising edge effects and maximising connectivity will need to be navigated. Such analyses must reflect the fact that for some species, habitat use within the home range is a poor guide to landscape permeability during dispersal [153,154]. When the most dispersal-limited species are considered, the limitations of land sharing become clear. For example, the two-toed sloth *Choloepus hoffmanni* uses shade cocoa farms for dispersal, but avoids pastures: this suggests potential benefits of land sharing at least for this species [155]. However, the more specialised and sedentary three-toed sloth *Bradypus variegatus* does not use shade cocoa for dispersal, but depends on contiguous forests and riparian forest buffers [155]. This finding mirrors that of studies using the sharing-sparing framework: the species that most need help in fragmented landscapes are those least likely to benefit from land sharing. This is likely to be even more true for species which are highly threatened or narrowly endemic, unlike the two sloths.

2.8. Political Implications

Critics of land sparing worry that the model could provide ammunition to boosters of industrialised, corporate agriculture, but there is scant (if any) evidence for this [20]. Anyone claiming their activities are land-sparing should be challenged to identify what land is being spared, what specific evidence shows that this will have more benefit for biodiversity than other available actions, and what they are doing to minimise any negative impacts of increasing yields. Land sparing properly conceived poses a considerable threat to entrenched interests, which may explain why there has been little corporate interest in the concept. What follows is my own personal view—perhaps best left out of data-driven papers, but appropriate in a perspective piece like the current article.

Taken to their logical conclusion, the results of land sparing-sharing studies suggest to me not only that conservationists should seek an end to agricultural expansion, but that we should advocate for shrinking the global footprint of agriculture to enable widespread habitat restoration and reduce extinction debt. To minimise negative social impacts, it is essential that smallholder farmers receive the support they need to provide for themselves without further expansion of cultivated land. Corporations already have sufficient resources to increase yields; the overwhelming need is to improve regulation, transparency and accountability to ensure social and environmental protection. Governments will need to confront the expansion of industrial agriculture, and close the agricultural frontier. Many producers lie somewhere on a spectrum from small to large: they will need a balance of support and regulation.

This stance is consistent with calls for much more of the Earth (perhaps half) to be devoted to nature conservation [106]—although this should not be taken to mean expelling people [78], nor conserving only remote and uncultivable areas [156]. It is consistent with calls for humanity to transition from an ideology of extractivism to a steady-state economy [105]. It is consistent with an ecocentric ethic that sees humans as just one species living alongside others [90]. The idea that there is no new land for farming should prompt a greater focus on stewardship of the land we are already using, and greater efforts to recover or restore degraded agricultural lands. The approach I suggest would place the greatest responsibilities on those who have the most power and resources: the largest landholders, agricultural businesses, and governments, while providing the greatest protections and support to those with the least power: smallholders, the landless and non-human species. None of these points are exclusive to a land-sparing perspective, but they are supported and reinforced by the findings of studies that have used the model. This is not a vision that will be achieved quickly, or easily, or everywhere, but it offers an alternative paradigm to that of tweaking farming practices and hoping that somehow this will be enough to deal with the biodiversity crisis.

3. Conclusions

The land sparing-sharing model provides a powerful way to understand how species respond to farming, and what is needed for their populations to persist into the future. It is underpinned by an ethic that seeks to minimise harm to wild animal and plant species. Insights from the model should be interpreted alongside those from social, political and economic methods. Empirical studies in a variety of geographies show that most species would have larger populations if a given amount of food is produced on as small an area as possible, while sparing as large an area of native vegetation as possible. This is especially true for species with smaller global ranges. Efforts to build on and extend the model to inform specific conservation decisions are to be encouraged. For example, more important than vote-counting to identify which broad strategy is best (sparing, sharing or intermediate) is to define land-use strategies that can ensure populations of all wild species in a region are sustained.

This article cannot cover every complexity, but I hope that it encourages better conversations about the pros and cons of different strategies along the land sparing-sharing continuum. In reviewing eight common criticisms or points of contention, I made the case that most of them are based on misunderstandings or unsupported assumptions. When the model is interpreted appropriately—as one part of an elephant, alongside insights from social science and the humanities—there is less need for disagreement than is often perceived. The point of the framework was to widen the set of options that conservationists should consider, not to narrow them. Moving towards a shared understanding of concepts, questions and data needed to answer those questions will be important in developing a more productive dialogue, and in working towards a world that has space not only for small farmers, poor urbanites and indigenous people, but for giant trees, tiny beetles, Chocolate-backed Kingfishers, and other wild species too.

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