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Countryside Biogeography: the Controls of Species Distributions in Human-Dominated Landscapes

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Abstract

Purpose of Review Countryside biogeography seeks to explain the distribution of wildlife in human-dominated landscapes. We review the theoretical and empirical progress towards this goal, assessing what forces control the presence, abundance, and richness of species in anthropogenic and natural habitats, based on characteristics of the landscape and the species themselves.

Recent Findings Recent modifications of species-area relationships that incorporate multiple habitat types have improved understanding of species diversity in countryside landscapes. Attempts to understand why species affiliate with human-modified habitats have been met with only partial success. Though traits frequently explain associations with human-modified habitats within studies, explanatory traits are only rarely shared between studies, regions, or taxa. Nonetheless, greater attention to the regional and climatological context of countryside landscapes has uncovered that (i) species that associate with human-modified habitats within landscapes tend to occur primarily in warm and/or dry biomes at regional scales and (ii) species that rely exclusively on human-modified habitats in cool or wet regions may be restricted to natural habitats in warm or dry regions.

Summary There remains a pressing need to determine how biodiversity can best be supported within landscapes to preserve nature and maximize ecosystem service benefits for humans. Future work in countryside biogeography must identify how land-use change interacts with other global stressors (e.g., climate change), determine how extinction debt and population sinks influence diversity, quantify the cascading effects of community changes on ecosystem services, and elucidate the evolutionary history and origins of species that today dwell in the countryside.

Keywords Anthropocene · Ecosystem services · Traits · Matrix · Fragmentation

Introduction

As human influence on Earth has expanded over the past millennia, an ever-greater proportion of the planet's surface

can be described as “countryside”—an intermixing of human habitations, agricultural lands, and remnant natural or near-natural habitats. Countryside biogeography seeks to understand the distribution of biodiversity across these human-dominated ecosystems [1]. In practice, countryside biogeography has been primarily focused at the landscape scale, attempting to elucidate the environmental forces that shape species distributions and community compositions. These forces have included variables such as the distance to protected areas, alternative local practices (e.g., planting crops in polyculture [2]), and wildlife-friendly landscape practices (e.g., maintaining nearby remnant vegetation [3]).

The discipline emerged in the 1990s to more holistically investigate wild, feral, and domestic species across all components of landscapes and ecosystems, including natural, semi-natural, and fully anthropogenic habitats [1, 4–6]. This epistemological lens differentiates countryside biogeography from previous traditions in that it shifts focus away from the patch paradigm that dominated

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conservation in the 1980s. This view, shaped by the strength and predictive power of MacArthur and Wilson's Theory of Island Biogeography [7], concentrated sampling on intact forest reserves and forest fragments of varying sizes: the active metaphor being that forest fragments are akin to islands in a sea of inhospitable anthropogenic land cover.

With greater scrutiny came increasing documentation of extensive biodiversity persisting, and in some cases thriving, within the human-modified "sea" of countryside habitats [4, 8, 9]. Species that relied on remnant fragments often readily dispersed through countryside habitats, making the countryside much more permeable to species movements than true islands surrounded by water [10]. As a result, the type of land use that surrounded fragments (i.e., the "matrix"; see Box 1) was shown to play a role in determining community composition *within* fragments [11–13]. More importantly, many individuals of native species were shown to complete their lifecycles entirely within these countryside habitats [13, 14], meaning a fragment-only focus overlooked a large portion of the habitat within landscapes. Together, the distribution and movement of biodiversity outside of native habitats brought into question the degree to which Island Biogeography provides an apt predictive framework for a landscape-wide understanding of biodiversity and called for greater attention for biodiversity in diverse countryside habitats [13, 15–18]. Today, the study of countryside biogeography and closely related disciplines are striving to provide predictive frameworks for understanding the changes experienced by biodiversity over the coming centuries [1].

We organize this review by first providing a theoretical grounding in how countryside biogeography theory differs from island biogeography theory. We then describe how empirical studies have documented (i) the environmental forces that determine biodiversity in the countryside and (ii) how distributions of organisms at the landscape scale reverberate to affect regional and continental species pools (and vice versa). Next, we examine the species-level properties (i.e., traits) that facilitate survival in countryside habitats versus natural habitats. Finally, we describe what is known regarding how species distributions in the countryside impact ecosystem functioning, as well as the ecosystem services provided to humans. We end by drawing attention to unanswered questions in countryside biogeography. Historically, there has been a strong bias towards agricultural and grazing landscapes in countryside biogeographic research, due in part to their prominence across the globe [19]. The examples we discuss draw primarily from such landscapes, but better integration of landscapes with substantial human habitation is clearly needed and will doubtlessly provide further insights [20].

Box 1: Defining "Matrix" in Countryside Ecosystems

Within the field of landscape ecology, the use of the word "matrix" can take on two alternative meanings. The first stems from metapopulation theory [21, 22] in which a species' "habitat" (locations that maintain its populations) is contrasted with the non-habitat "matrix" (which it does not use but can move through to colonize new habitat patches). This definition is implicitly species centric, as what constitutes habitat versus matrix will differ between species. The other widely used definition is "matrix" as "other," referring to any land cover type(s) in the landscape other than the focal one (typically primary natural habitat), or alternatively the single major land cover type in which patches of some other focal habitat are embedded [23, 24]. This definition is landscape centric, with the implicit assumption that the focal habitat is the most ecologically valuable type in the landscape. This can be subjective, with different researchers potentially classifying alternative parts of the landscape as matrix. In the landscape-centric version, it is reasonable to speak of "matrix habitats", whereas in the species-centric version such a phrase is oxymoronic.

The two meanings of the matrix closely align with the "pattern-oriented approaches" and "species-oriented approaches" for studying the biology of human-modified landscapes discussed by Fischer and Lindenmayer [17]. Nevertheless, these two definitions are still often used interchangeably in the literature or simply acknowledged simultaneously in the same definition [24]. For those species that primarily associate with natural habitat types, the definitions are identical. The term "matrix", however, becomes problematic for species that associate strongly with human-modified land covers. Further, human-modified land covers may contain many ecologically distinct habitat types (e.g., shade coffee versus pasture) and, as such, a single designation of "matrix" risks obfuscating their ecological differences. A similar single designation of "habitat" in a landscape is equally problematic [17]. Ultimately, a conceptual dichotomy between "matrix" and "habitat" undercuts the natural continuum in habitat use experienced by species and the diversity of land covers contained within landscapes (Fig. 1). A strict dichotomy may also psychologically diminish the probability that researchers devote the same attention to sampling in the "matrix" like they would in "habitat", leaving scientifically "neglected communities" in anthropogenic habitats. While the term matrix is rarely used in countryside biogeography, the term is perhaps still useful for communication and as a shorthand. For these reasons, when we use the term, we have adopted the species-centric definition of matrix as "non-habitat" throughout this review, while acknowledging that there is no clear-cut threshold for when a location transitions from "matrix" to "habitat" (Fig. 1).

Countryside Biogeography Theory

Understanding the different responses of biodiversity to habitat change is a key to improving conservation. Based on the equilibrium theory of island biogeography [7], there is a well-known relationship between the size of a habitat and the number of species in that area [25]. These traditional species-area relationship (SAR) modeling approaches consider native habitat patches (or nature reserves) as islands, in which the matrix surrounding them is a "sea" of completely inhospitable habitat. Such models have been widely used to compare species diversity patterns when regions differ in area, predict the response of species richness to native habitat area loss, and estimate species extinctions across a wide variety of systems and scales [25–27].

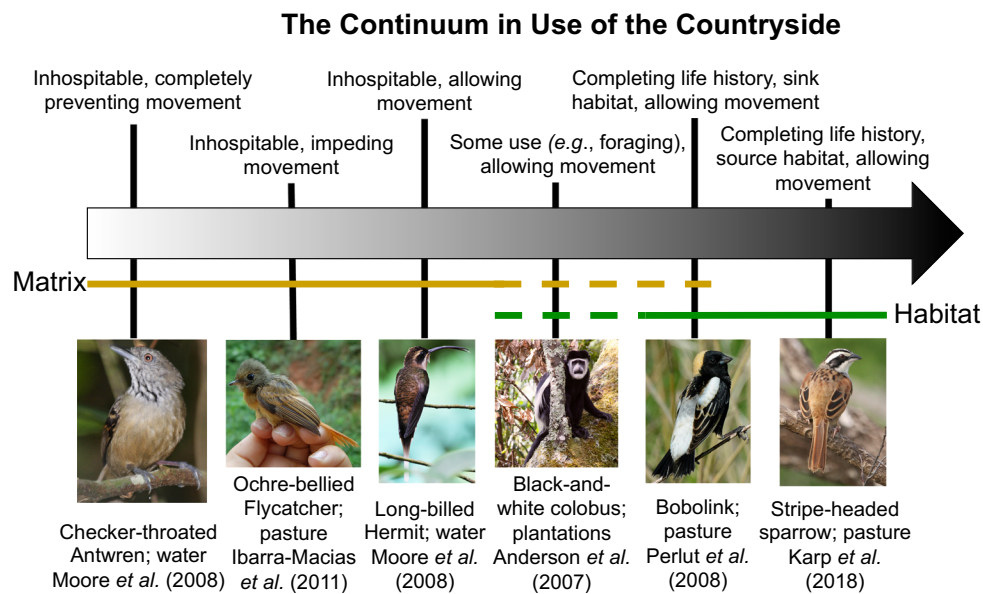


Fig. 1 Distinguishing between “matrix” and “habitat” is useful conceptually, yet species interact with multiple land covers in the countryside along a continuum. Each species will perceive each land cover available in a landscape differently, as somewhere along the matrix-habitat continuum. We illustrate this continuum, in terms of how individual species respond to various forms of non-primary land cover

based on the degree to which they can move through, acquire resources and maintain viable populations within it [94, 172–175]. Green and yellow lines depict how each species perceives the specified land cover along the matrix to habitat continuum, with dashed sections illustrating where the strict dichotomy between the two becomes hazy

Yet, the overextension of this framework to predict species loss within human-dominated landscapes has frequently been questioned, as biodiversity responses regularly defy patterns predicted by the island biogeography theory [28, 29]. Criticism towards applying the theory of island biogeography to countryside ecosystems stems from the vast empirical evidence that many species are not constrained to fragments of their native habitat and that the anthropogenic habitats surrounding remnant native habitat fragments can play an important role in the conservation of biodiversity [1, 30]. As a result, studies that quantify the effects of the land covers surrounding focal patches better explain community composition than those that take a binary “habitat/non-habitat” approach [30]. This is because the surrounding countryside habitats can facilitate recolonization of native habitat fragments [31] and also support significant levels of biodiversity within them [4, 8, 32–36]. In fact, according to the IUCN reports of habitat use, at least 47% of 10,061 extant bird species use human-modified habitats to some degree, with 32% using agricultural habitats specifically [37].

In response to these limitations, new, holistic methods for predicting diversity patterns are emerging for countryside ecosystems (Box 2). These multi-habitat SAR models adapt the island biogeography paradigm to one that incorporates multiple habitats and their associated biodiversity [38–41]. Such models tend to be calibrated based on the extent and/or quality of both native and human-modified habitats as perceived by the taxon. Overall, by accounting for species persistence in human-modified habitats, these models have proven to

outperform traditional SAR approaches when describing the number of species in countryside landscapes, both at local and regional scales [42–45], although the improvement was especially marked at the local scale. Specifically, empirical studies have suggested that as the sampling scale increases, the effect of land use on biodiversity patterns tends to decrease [44]. That is, at very small scale, the habitats are homogenous and one either considers species entirely within native or entirely within a human-modified habitat. In contrast, at larger scales, any sampling unit is a mixture of both habitats and the effect of land-use change on the SAR decreases [45].

Multi-habitat SAR approaches still rely on very simplistic assumptions, such as that species are randomly distributed across the landscape and that species increase with habitat area independently of how fragmented the habitat is (although some SAR models specifically targeting this issue have been developed [46]). In general, these assumptions appear justified, as empirically the extent of a given habitat and the composition of the landscape tend to better explain diversity than isolation or configuration [47]. While further improvements remain, multi-habitat SAR models provide valuable insights into biodiversity dynamics in countryside ecosystems. Notably, recent works using the countryside species-area relationship (cSAR) framework allow for more precise detection of community response (e.g., specialists versus generalists) to land-use change [48]. These models are being used to help address whether biodiversity protection is best achieved by pursuing wildlife-friendly farming methods that may sacrifice yield and require more land to be converted (land sharing) or by intensifying yield within

farms in the hope that this will decrease pressure to convert natural habitats (land sparing) [49]. However, preliminary evidence suggests that land sparing and land sharing are not necessarily mutually exclusive at larger scales, since their potential impacts on biodiversity are context dependent [48]. For example, in Portugal, land-sparing strategies present some opportunities, as there is scope to intensify existing agricultural areas to increase yields [48]. However, such a strategy is likely to mainly benefit biodiversity in the center and north of Portugal, regions already undergoing extensive farmland abandonment. In contrast, most of the south of Portugal is characterized by *Montados*, a well-established agro-forestry system that supports high levels of biodiversity and ecosystem services (i.e., land sharing strategy) [48].

Current theoretical frameworks, like the cSAR, tend to focus on species as the units of biodiversity, measuring changes in ecosystems by understanding changes in species counts. Yet biological diversity is a multifaceted construct, which includes phenotypic variation within and between species and diversity in how species interact within one another and their ecosystems. Future theory must aim to evaluate the links between species in human-dominated ecosystems, so as to measure both species diversity and ecosystem functioning. Doing so will provide a better theoretical understanding between changes in biodiversity, ecosystem functioning, and human well-being [50].

Box 2: Modeling Species Diversity in the Countryside

The species-area relationship (SAR) represents species richness (S) as a function of sampling area (A), where larger areas generally support more species. It is commonly given as a power function [51]:

$$S = cA^z,$$

where S is the number of species in area A and c and z are the fitted parameters. Since the year 2000, a number of SAR-based models have been put forward that considered both habitat area and habitat composition to explain species richness (hereafter called multi-habitat SAR models). Tjørve [38] proposed a framework to build species diversity models in multi-habitat landscapes by combining species-area curves for different habitats. A year later, Triantis et al. [39] proposed the choros model, where the variable “area” is replaced by the variable “choros” (K), which arises as the result of the multiplication of the number of different habitats in an area (H) and the size of that area (A). A few years later, the countryside SAR model proposed by Pereira and Daily [40] was the first to describe differential habitat use by different species. It introduced a parameter, h_{ij} , reflecting the habitat affinity of a species group i to a habitat type j . Here, the richness of each species group i is given by:

$$S_i = c_i \left(\sum_{j=1}^n h_{ij} A_j \right)^z,$$

where n is the number of modified habitat types and A_j is the area covered by habitat j . Then, the total number of species in the landscape is given by the sum of species in each group. More recently, Koh and Ghazoul [41] proposed the matrix-calibrated SAR, where matrix effects are incorporated in the SAR framework by partitioning the z value of the power model into two components: γ , a constant describing the unsuitability of the matrix and σ , the sensitivity of the taxon to the transformed habitat.

Environmental Controls of Species Distributions in Countryside Landscapes

A variety of conceptual models have been proposed to explain how organisms distribute themselves across countryside landscapes [16, 52]. Pulsford et al. [16] outlines five models, all of which differ explicitly in how they consider human-modified habitats. As discussed above, island biogeographic theory [7] ignores everything except the focal natural habitat type, considering only the patch size and isolation to drive biodiversity dynamics. The habitat amount hypothesis postulates that it is total (semi-natural or natural) habitat amount within an area—irrespective of configuration and isolation of discrete patches—that determines species abundances and diversities [53]. The matrix tolerance model [54] shifts focus to modified habitats, hypothesizing that a species' abundance in a human-modified landscape will depend entirely on its ability to use the modified habitats—which can mean either persisting within or just moving through these land covers. The matrix quality model [55] extends the matrix tolerance model, arguing that not all modified habitats are the same and thus species will vary in their ability to use different modified habitats (e.g., shade coffee versus sun coffee versus forest). Finally, the continuum model [56] rejects the idea that modified habitats should be binned into discrete categories, instead arguing that species abundances in modified habitats will depend on underlying gradients in environmental conditions. All pastures, for example, are not the same: as tree density incrementally increases in pastures, so too may nest site availability and microclimate refugia, increasing abundances of tree-nesting or cool-adapted organisms. In practice, each conceptual model may prove predictive in different situations—though predictions from strict island biogeography are rarely upheld in the countryside [16, 52, 57] despite their strong explanatory power in true island systems [15, 58]. Complete tests of all alternative hypotheses are rare. However, in a study of Australian amphibians and reptiles, most species did not respond to discrete land-use types per se (e.g., forest versus type of anthropogenic land cover). Instead, the majority of species responded in species-specific manners to underlying environmental gradients (i.e., the continuum model), which may themselves be influenced by land-use type and landscape structure [16]. While modeling species responses to environmental gradients should be the goal for basic science describing and predicting community composition in anthropogenic habitats, these models can be extremely data intensive. Parameterizing and implementing continuum models for conservation decision-making may be time and cost prohibitive and unnecessary [52], especially if model study systems can be used to understand how underlying environmental gradients tend to correlate with land-use types.

Nevertheless, that underlying environmental gradients and resources are the primary forces controlling abundance

provides scope for fine-tuning anthropogenic habitats to support biodiversity. Anthropogenic landscapes contain a multitude of environmental gradients (microhabitat structure, microclimate, resource availability), all of which can vary across natural habitats, semi-natural habitats, crop fields, and zones of human habitation. Importantly, both naturally and through management, these environmental gradients also vary within land-use types. As a result, common strategies to conserve biodiversity in agricultural landscapes include reducing local management intensity, increasing resources used by wildlife, and facilitating heterogeneous landscapes. Although local management is usually implemented at the farm scale, the impacts of agricultural intensification operate at scales from fields to regions. Therefore, conserving biodiversity in these landscapes requires a multi-scalar approach [59–61], as some taxa respond more strongly to local management, while others respond to landscape-level features. Depending on species traits and environmental context, controls on biodiversity may be stronger at local or landscape scales, and effects can interact across scales [62, 63].

Within the countryside, local practices that support biodiversity typically focus on adding vegetative cover, increasing environmental heterogeneity, and reducing external inputs (e.g., pesticides and fertilizers). For example, one study found that, across a range of local management practices, lower-intensity management (e.g., organic practices, reduced application of pesticides or fertilizer, and planting flower strips) increased diversity of plants and invertebrates, but not vertebrates [60]. Organic management may include some or all of these practices and often supports higher species richness and abundance compared with conventional systems [64, 65]; however, a focus on the outcomes of specific practices may be more informative [66]. Within fields, crop diversification and the maintenance of non-crop vegetation benefit arthropods, birds, and bats by supplementing available on-farm food resources and creating diverse habitats [2, 59, 67, 68].

The addition or restoration of perennial habitat, such as hedgerows and scattered trees, can support biodiversity by creating habitat, supplementing resources, and increasing matrix permeability in systems where trees have been removed [69, 70]. For example, isolated fruiting trees in agricultural landscapes are an important resource for tropical frugivorous birds, and their incorporation into farm boundaries or hedgerows could bolster biodiversity in the countryside [71]. Hedgerow structural components (i.e., complexity, height, and width) typically determine conservation value for taxa [72]. Hedgerow connectivity is also important for mobile species, such that concerted replication at the landscape scale can boost pollinator diversity to levels similar to some natural communities [69]. Areas near scattered trees support higher biodiversity than open matrix areas and, for many taxa, levels of species richness and abundance that are similar to natural habitat [73, 74]. A recent meta-analysis supports the benefits

of scattered trees for arthropods, vertebrates, and woody plants, but not for herbaceous plants, highlighting differences in effects among taxa [73]. Indeed, incremental increases in local tree cover within tropical agriculture provides benefits for vertebrate diversity saturating at or near that held within forest reserves [8]. Scattered trees may work especially well on grazed lands, such as silvopastoral systems, where they can improve microclimatic conditions for other species and may comprise diverse tree communities that facilitate forest regeneration [75].

Supporting wildlife across countryside habitats, be it in fragmented remnant vegetation or within farms themselves, and conserving large tracts of natural areas as preserves are both essential strategies for biodiversity conservation [76]. Wildlife-friendly, on-farm practices and surrounding semi-natural environments function synergistically to improve habitat quality and support higher dispersal rates, as well as higher biodiversity, at greater distances from semi-natural habitat [77–79]. However, the scale and threshold of (semi-)natural habitat amount needed to guarantee the maintenance of biodiversity vary by taxa and region [79–81], with mobile species in higher trophic levels generally responding to landscape structure at larger spatial scales [82, 83]. The degree to which large tracts of land are needed lies in part on whether species and biodiversity as a whole respond primarily at local or landscape scales. The answer remains contentious, with evidence supporting both viewpoints in alternative study systems and analytical frameworks [60]. In addition to changing the amount of habitat, landscape modification has also increasingly fragmented semi-natural habitats. The resulting creation of edge habitat can have either positive or negative effects on biodiversity [84]. In contrast, landscape heterogeneity (in some ways the opposite side of the fragmentation coin) tends to have a positive effect on biodiversity conservation [85–88].

Recent literature has addressed the degree to which landscape attributes moderate the effects of local agricultural management practices on biodiversity outcomes. Local environmental diversification may bolster biodiversity in simple landscapes (i.e., landscapes dominated by a single anthropogenic land cover) with a minimum threshold of semi-natural habitat that supports species pools, but may offer limited benefits in already heterogeneous landscapes that currently support high levels of biodiversity [89, 90], suggesting that local diversification and semi-natural habitat can sometimes be interchangeable [62, 66]. However, the efficacy of local agricultural management practices on biodiversity gains likely depends on the composition of regional species pools, such that diversification practices may bolster species richness more in complex than simple landscapes [59].

The role of habitat fragmentation, as of yet, have not been well addressed in countryside biogeography, in part because the effects of fragmentation of human-modified habitats (in addition to native habitats) is difficult to measure in most systems

where human-altered habitats are fairly continuous. Studies in systems where the independent effects of fragmentation and habitat amount can be robustly assessed offer a rich arena for future work [91]. To date, and perhaps counterintuitively, the effect of fragmentation in most systems appears to be weakly positive for biodiversity [92], though this remains hotly contested and varies substantially from system to system.

One important observation is that though many species may persist in countryside habitats, community composition often strongly differs between undisturbed protected areas and countryside habitats, including embedded forest fragments [93, 94]. These trends complicate an ongoing debate regarding the merits of enhancing the conservation value of countryside landscapes (land sharing) versus intensifying agricultural production in countryside habitats while preserving more land in ecological reserves (land sparing). A burgeoning literature continues to grapple with these two options, with some studies concluding that land sparing is essential to preserve forest-dependent species [95] and others arguing that spatially aligning conservation and food production can help achieve both production and conservation goals [96]. Although land sharing approaches that increase yields and minimize negative impacts to biodiversity do exist, these approaches are system specific and are influenced by contrasts between production and endemic systems and the feasibility of adopting and implementing these solutions [97]. Studies that track species persistence over longer time scales may help reconcile the debate, with the relative merit of each approach shifting based on the local conservation and production goals [76]. Both land-sharing and land-sparing approaches are likely needed to safeguard species. Countryside landscapes can be managed for conservation and complement protected areas by increasing habitat connectivity and allowing for the movement of species and ecological processes [98].

Anthropocene Biogeography and the Connection Between Local, Regional, and Global Diversity

While on-farm practices and landscape heterogeneity can help support biodiversity represented from within regional species pools, human influences are also causing the species pools themselves to shift. Indeed, as the environmental forces that shape distributions at the local and landscape scale become better understood, there is growing emphasis on uncovering how larger-scale regional and global processes determine species pools in human-dominated landscapes. International trade and transportation networks are connecting distant biogeographic realms and increasing the size of regional species pools [99, 100]. Human history and economic distance [99] are therefore beginning to swamp the effects of evolutionary history and geographic distance in determining species pool structure. For example, among non-native birds that colonized new areas before the twentieth century, the majority moved from Great

Britain to colonial dominions of the British Empire [101]. The dissolution of ancient biogeographic barriers means that the broad scale biogeography of the Anthropocene is in some ways more environmentally deterministic. For example, assemblages of gastropods are no longer sorted into seven geographic clusters defined by continental separation, but are instead primarily organized into two clusters defined only by tropical versus temperate climate [100].

What remains to be seen is whether anthropogenic land-cover change is helping to drive the dissolution of these ancient biogeographic realms. In short, is countryside biogeography reverberating up to regional and global scales? Preliminary evidence does suggest that by creating consistent environmental conditions irrespective of the natural biome, human land uses create novel anthropogenic biomes (“anthromes” [102]) that favor fortuitously pre-adapted species, sometimes from distant corners of the globe. A small cadre of birds repeatedly succeed in agriculture and urban environments, and invasive species tend to associate with modified habitats rather than natural ones [103]. Many Neotropical birds that affiliate with agriculture tend to be absent from Neotropical forests and have biogeographic ranges that overlap with drier climate zones—hinting that they may have evolved in drier grassland and shrub land biomes and only colonized forested regions once humans created open habitats there (Fig. 2) [104]. Further, adaptations for survival during repeated environmental disturbances (e.g., forest fire and hurricanes) may render entire regional assemblages more resilient to anthropogenic change [105].

Documenting how the “rules” of countryside biogeography change across larger-scale natural environmental gradients (e.g., climate gradients) is needed to address the generality of ecological rules and identify predictable contingencies [47, 106]. For example, are countryside habitats typically inhabited by diverse fauna or are there some climate zones or ecoregions in which the countryside is especially depauperate in comparison with natural habitats? Studies that clarify these or similar questions will further help to identify how multiple global change drivers (e.g., land-use and climate change) might interact together to shape future biodiversity. Recent work exploring land-use and climate gradients suggest that habitat conversion may synergize with climate warming and/or drying to drastically change community composition [94, 107–110]. For example, bird communities are most strongly affected by drought in fragmented natural habitats [108]. But the effects of habitat conversion on communities may diverge in different regions: in the lowland tropics, natural forest and human-dominated habitats share only 40% of their amphibian species, whereas in temperate zones over 90% of species occur in both habitats [111]. Ultimately, researching the influence of classical biogeographic variables on landscape-scale countryside biogeography will help upscale community level data to predict how communities will respond under future scenarios of land-use [112] and climate change.

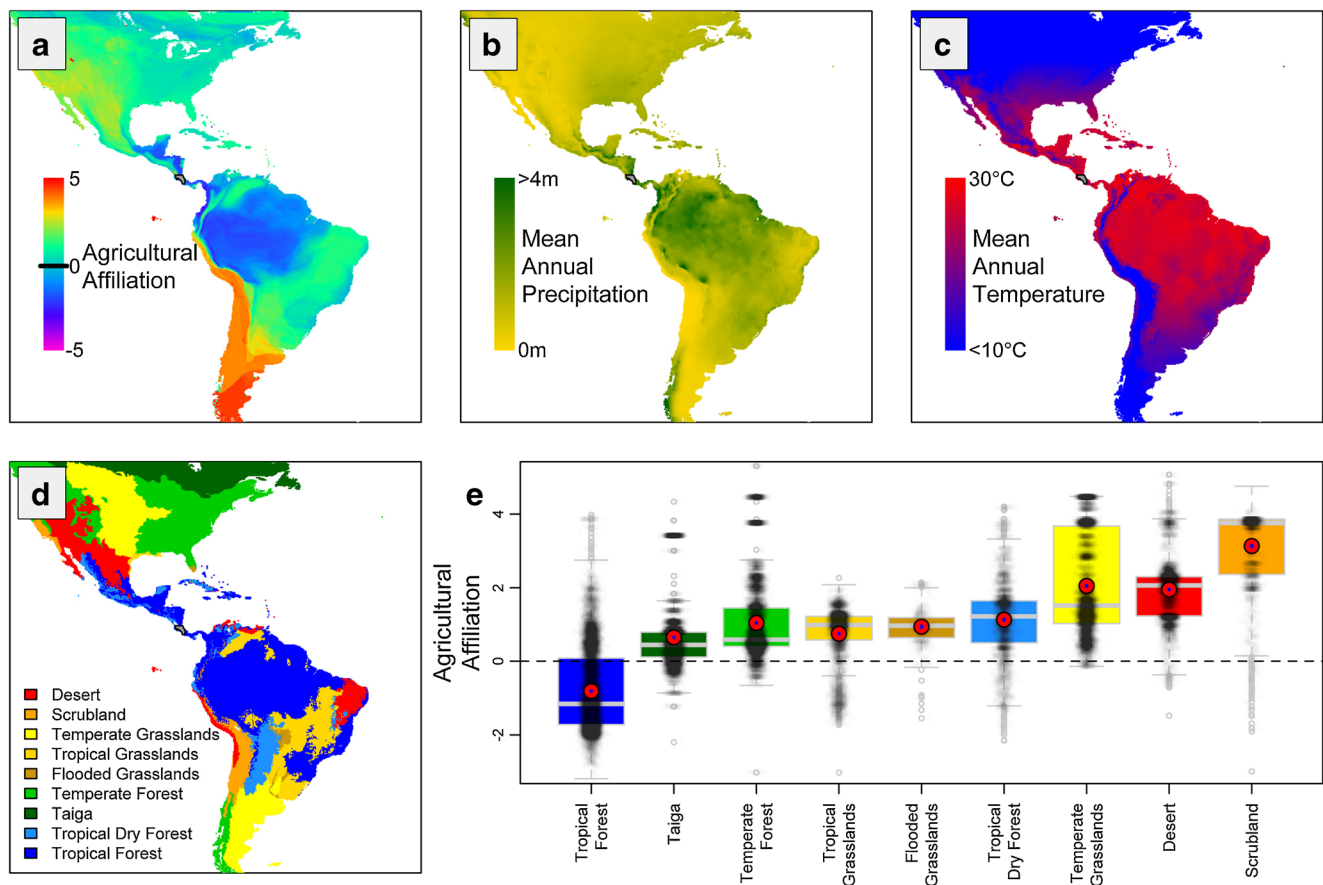


Fig. 2 Within a given landscape, birds that are found in human-modified habitats, like agriculture, come from different biomes and climate regions than those found in natural habitats. For example, agriculture-associated birds within four study landscapes in Costa Rica tend to have ranges that overlap with drier biomes across the western hemisphere. **a** Map depicting the average agricultural affinity of Costa Rican species whose ranges overlap with each depicted location on the globe. Blue indicates that most species with ranges overlapping a location occur primarily in forest reserves in Costa Rica, while orange and red indicate that most species occur in pastures, coffee, or banana plantations within Costa Rica. **b** Annual precipitation correlates strongly with the expected

habitat affiliation of the birds, while **c** temperature plays only a secondary role. **d** Major biomes across the western hemisphere. **e** Box plot depicts median and interquartile ranges of average agricultural affiliation in each of the major biomes of the western hemisphere (colors as in **d**); means are marked by red points. The dashed line indicates equal affiliation with forest and tropical agriculture. In panel **e**, each semi-transparent black point represents a 1/3 degree by 1/3 degree grid cell, jittered to better show the distribution of the data. Costa Rica (where the habitat affiliations are generated) is indicated in gray in all maps. Figure reproduced from [104]

While most previous work on the role of climate within the context of the countryside has been conducted on endotherms (especially birds), the mechanistic underpinnings that link biological consequences of habitat conversion to larger-scale biogeography are particularly transparent for ectotherms. The role of temperature appears supreme in defining ectotherm associations with human land uses in complex landscapes, where species' critical thermal maxima on average explain 38% of the variation in whether amphibian species associate with natural forest environments or lands cleared for human uses such as pastures and agriculture [113]. This link between thermal physiology and association with human land-uses causes complex ramifications at broad spatial scales. Frogs [114], lizards [110], and beetles [115] extend

their elevational range upslope in human-dominated habitats, occupying geographic space that they do not in the natural forest.

The repeated selection for individual species or consistent types of species in human-dominated landscapes across the globe is causing biotic homogenization [116, 117]. The spatial loss of unique assemblages over geographic space and natural environmental gradients is particularly stark in landscapes with the most intensive forms of agriculture [118, 119]. Concerns of homogenization bleed above the species level: even when identical species are not shared between distant locations, human domination of landscapes favors the same evolutionary lineages, meaning that phylogenetic homogenization still occurs [111, 120].

Species Traits and Countryside Distributions

One key to describing the distribution of species in the countryside is to determine which species traits confer an advantage for survival in alternative land covers. To garner the latest evidence for which traits determine species distributions in agricultural landscapes, we conducted a vote count of empirical studies published within the last 10 years (2008–2017) that investigated animal traits along an agricultural intensification gradient. We searched all articles in Web of Science (<https://www.webofknowledge.com>) using the following search query: (“trait*” or “guild*” or “phylogen*” or “functional group”) and (“countryside” or “land-use” or “land use” or “agricultur*” or “anthropogenic” or “habitat modification”) and (“distribution” or “abundance”). We considered significant relationships to be those with $p < 0.05$.

Based on this review of recent trait-based publications in countryside biogeography, the number of publications on this topic has steadily increased over the past 10 years (Fig. 3), focused especially on birds and insect pollinators. Dietary guilds in particular often exhibit variable responses to agricultural land-use change (Fig. 4). Birds, frugivores, insectivores, and nectarivores tend to decline while carnivores and granivores increase in agriculture [121, 122]. Almost all dietary guilds exhibit declines in response to agricultural land-use change in the limited number of studies on mammals [123]. Studies measuring diet breadth of invertebrates found no patterns in responses of generalists, but a general trend of declines in specialist invertebrates over gradients of agriculture [124]. Generally, human-dominated landscapes may promote

invasive species that have a greater dietary breadth as compared with native species [123].

Reptile and amphibian species that persist in hotter agricultural land uses consistently have larger body sizes and higher critical thermal maxima [113, 114] because body size is directly related to thermal tolerance [125]. Meanwhile, bird, mammal, and invertebrate species that migrate or disperse large distances tend to fare better in agriculture than non-migrants or short-distance dispersers [126–128], possibly because they can better track seasonal resources and adapt to land-use change [14, 129].

Species with high reproductive rates may also be better able to persist in agriculture because they can better compensate for increased mortality in a lower-quality habitat [130], but studies of reproductive effort in relation to agricultural land use have found inconsistent relationships [127, 128]. Notably, bird species with longer incubation and fledgling periods (which is empirically related to high juvenile survival) increase in abundance in farmland, suggesting that low juvenile survival may be a mechanism that increases species vulnerability to land-use change [130].

Recent work has uncovered that species responses to habitat conversion are frequently phylogenetically conserved, meaning that closely related species tend to all associate with (or avoid) human-modified areas [111, 131–134]. Further, agricultural expansion and intensification particularly threatens more evolutionarily distinct species, while species from more recently diversifying clades are able to utilize agricultural habitats [131, 135, 136]. Why this is remains unclear.

Fig. 3 Number of publications focused on how species' traits relate to agricultural land-use change from 2008 to 2017

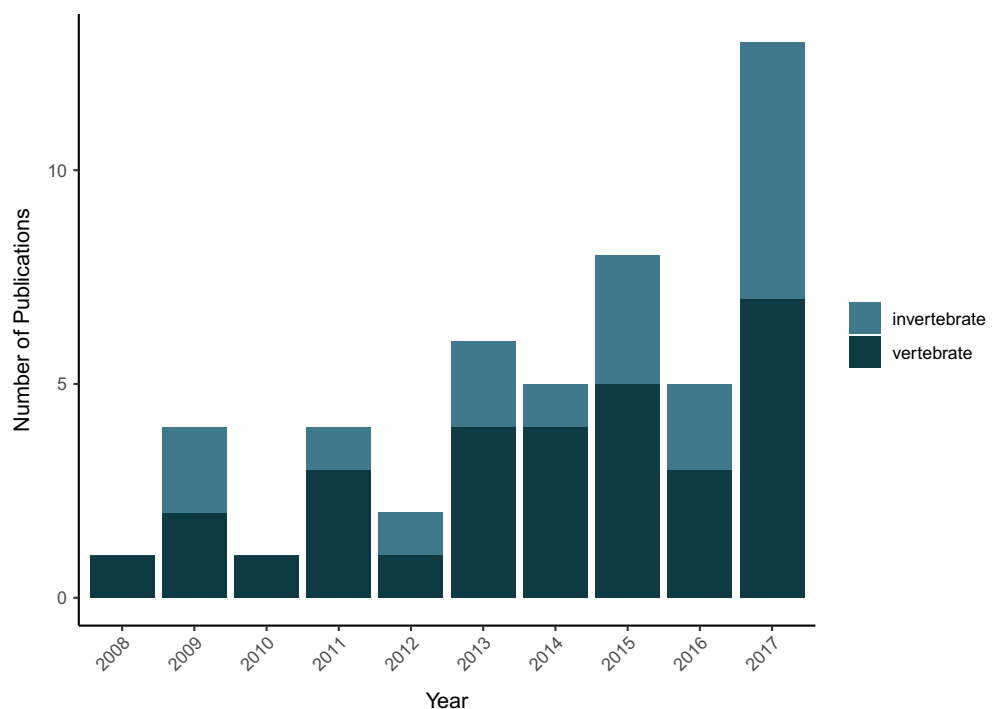
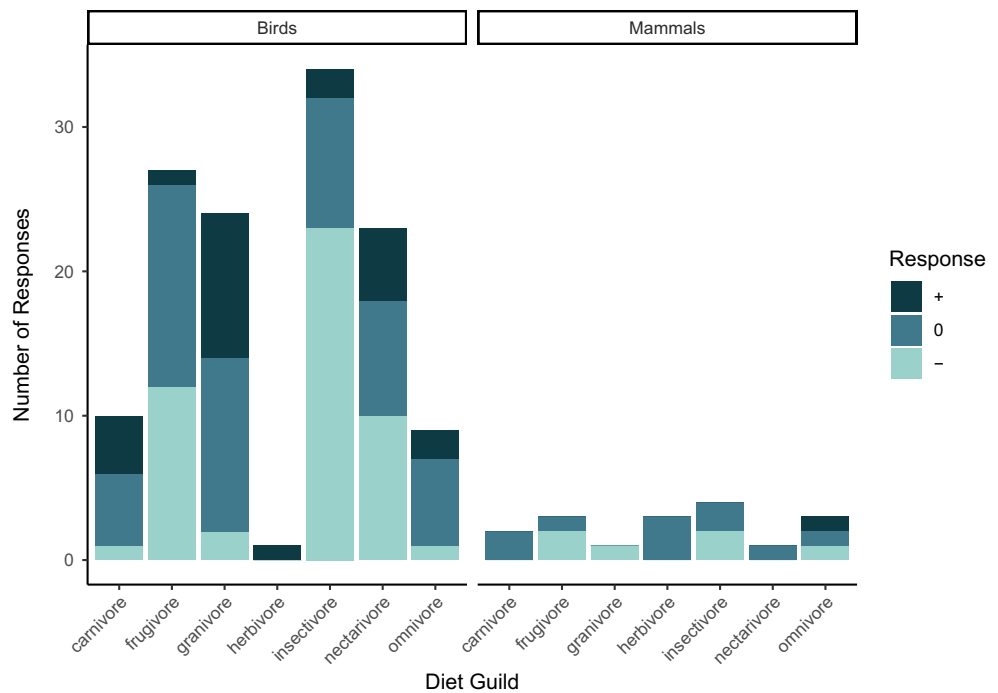


Fig. 4 Vertebrate responses to agricultural land-use change, organized by dietary functional guild and taxon (birds vs. mammals). Non-zero responses are those with $p < 0.05$. No studies of reptiles and amphibians included dietary traits because almost all are insectivores



Uncovering trait-based generalities in countryside biogeography may have been slowed by several recurring methodological challenges. Grouping species into coarse categories such as dietary guilds may not accurately represent species attributes, as many species utilize more than one type of food [137]. Studies often assess changes in abundance within functional groups [138, 139], which can lead to incorrect inferences about relationships between traits and land use if one species has a disproportionately high abundance, and thus large effect, within its functional guild. This will result in more studies reporting significant trends (in either direction) than is appropriate based on the data and may contribute to the variation in directionality reported between studies (Fig. 4). These issues can be addressed through species-based (rather than guild based) assessments of countryside distributions [140].

Overall, recent studies have found few general patterns in the traits that determine species distributions in anthropogenic landscapes, and there are many gaps in trait-based research in countryside biogeography. This issue is highlighted by two recent analyses examining the predictive power of traits across multiple landscapes, which found surprisingly little consistency in which traits seemed to determine responses [124, 141]. Future studies must increase breadth and depth of trait-based research. Broadening should take the form of considering physiological traits of endotherms and a larger diversity of taxa, including microbes. Increasing depth should occur by addressing the reasons for inconsistency between studies, manifest by interactions between traits and the environment or two-way interactions between traits [142].

Ecosystem Function and Ecosystem Services

Wild species in countryside landscapes can provide significant benefits to private landowners by recycling nutrients that replenish soil quality, pollinating crops, and controlling damaging insect pests, weeds, and crop diseases, [143]. In the USA alone, the natural enemies of crop pests prevent > US\$4.5 billion/year in crop losses [144], and animal pollinators are directly responsible for ~35% of global food supply [145]. Yet, wild species can also plague farmers; for example, by consuming or competing with crops and spreading diseases [146]. Thus, over the past decade, ecologists have begun exploring relationships between biodiversity, ecosystem services, and ecosystem disservices in natural and farming landscapes [147].

Overall, biodiversity seems to correlate with ecosystem services, but significant heterogeneity exists among different services [148]. For example, pollination may be more directly linked to biodiversity than pest control [147], perhaps because biodiverse communities of natural enemies may contain more species that consume each other [149, 150]. Confronted with such complexity, ecologists are again turning towards trait-based analyses for predicting the relationship between biodiversity and ecosystems services in human-dominated landscapes [151]. Indeed, because traits modulate species' impacts on ecosystems, the diversity of traits in a community is often a better predictor of ecosystem function and services than local species richness (e.g., [152]).

Traits can also help ecologists understand the relative resilience of different ecosystem services to land management and species loss. For example, one study found that larger bees and dung beetles were both more vulnerable to disturbance and

more efficient pollinators and nutrient recyclers than their smaller counterparts, compromising the potential resilience of pollination and nutrient recycling services [153]. On the other hand, because abundant bees are responsible for the bulk of pollination [154], few species are needed to provide pollination services locally. This is not to say that pollinator biodiversity is unimportant; by accounting for crop specificity and spatial patterns of species turnover, Winfree and colleagues [155] calculated that at least 60 bee species were needed to meet a 50% pollination threshold across only 15 sites and 3 crop species.

Looking forward, a major frontier for countryside biogeography will be linking changes in land management to changes in biodiversity and ecosystem services through trait-based analyses [151]. Indeed, combining information about the traits that dictate species responses to disturbance gradients with information about the traits that control species effects on ecosystems holds real promise. Thus far, most studies instead simply correlate changes in ecosystem-service-provider abundance or ecosystem services with local and landscape-level management gradients. For example, both local practices (organic agriculture, farm-level diversification with hedgerows, flower strips, etc.) and landscape attributes (surrounding nesting or foraging sites) are associated with pollinator abundance, richness, and pollination services [2, 156]. For pest control, however, semi-natural vegetation in the surrounding landscape is often associated with natural enemy abundance [157], but may also enhance pest populations, leading to complicated pest-control dynamics [158, 159].

Identifying and reconciling such tradeoffs is another emerging focus for countryside biogeography, especially when designing strategies to manage biodiversity and multiple ecosystem services. For example, the “landscape-moderated biodiversity versus ecosystem service management hypothesis” posits that fragmented landscapes optimize movements of habitat generalists between natural habitat remnants and farms, bolstering ecosystem service delivery [160]. Increasing the farmland-natural habitat interface, however, is in direct conflict with known strategies to conserve more vulnerable, forest-dependent species. In other cases, tradeoffs are widely perceived, but not necessarily valid. For example, widespread concern that wildlife vector foodborne disease has led to significant habitat removal near produce farms in California [161]. By evaluating multiple services and disservices along landscape gradients at once, however, Karp and colleagues [161, 162] found that non-crop vegetation was associated with elevated pest control and arthropod biodiversity but no higher food safety risk.

Next Frontiers in Countryside Biogeography

Over the last two decades, substantial progress has been made in delimiting the factors that control species distributions at the landscape scale, be they characters of the environment

(distance from reserves, vegetative structural complexity, intensive versus diversified farming practices) or the species themselves (body size, trophic position, physiology). We point towards four areas for investigation over the coming two decades.

- (i) *How will land-use and climate change interact to structure species distributions in the countryside?*

Habitat conversion and climate change together likely represent the two greatest threats to global biodiversity. How these forces will interact together remains a major source of uncertainty. Countryside biogeography must consider how ongoing climate change will affect species' landscape-scale distributions [163]. Changing climate conditions could make countryside habitats more or less hospitable for species that use them as habitat, as well as more or less hospitable for species that use them as a conduit to connect habitat patches [125, 163]. Shifting climates might also lead to redistributions of species. The majority of this work has taken a macroecological approach and focused on the possibility that habitat conversion and fragmentation will impede range-level redistribution, especially for species that cannot easily travel through human-altered land covers (e.g., [164]). However, these redistributions may occur at the landscape scale, as open countryside species come to rely on cooler forested habitats to track their thermal niche (i.e., habitat switching [104, 114]). Such habitat switching due to climate change may result in increased competition in natural habitats. Alternatively, climate-driven redistributions may occur across landscapes, resulting in colonization of countryside landscapes from nearby species pools. Such colonization could re-balance the distribution of biodiversity in anthropogenic versus natural habitats, especially if certain habitats or species types tend to be faster colonizers, with knock-on consequences for ecosystem functions and services.

- (ii) *How do land-management practices and landscape context cascade to affect biodiversity and go on to determine ecosystem services?*

A growing body of knowledge indicates that increasing biodiversity in wild and managed ecosystems can enhance the functioning of ecosystems and their contributions to people [147, 148]. Historically, connections between biodiversity and ecosystem services were explored in short, small-scale experiments. A key frontier in countryside biogeography is scaling up these studies across landscapes and over longer time scales to examine realistic connections between biodiversity, ecosystem services, and human well-being. Indeed, it is now widely recognized that the non-random changes in community composition that accompany global change can have reverberating implications throughout ecosystems [165].

While studies connecting biodiversity and ecosystem functions at large temporal and spatial scales are becoming more common [166], very few studies have traced how realistic changes in biological communities across landscapes ultimately affect ecosystem services and rural livelihoods. For example, small-scale studies may conclude that bee biodiversity plays a limited role in pollination due to the overwhelming importance of a few abundant species [154]. Yet, accounting for natural changes in bee communities across landscapes and cropping systems (β -diversity) highlights the rich diversity of species needed to provide pollination at larger spatial scales [155]. Similarly, the importance of diversity is accentuated when multiple ecosystem functions and/or services are considered simultaneously [167]. A promising path forward for countryside biogeographers may be leveraging trait-based analyses to develop predictive frameworks for relating the cascading effects of changing environmental conditions on biological communities, ecosystem services, and their ultimate impacts on human well-being [151].

(iii) *Are countryside habitats a sink? Are species capable of persisting in the countryside over the long term?*

Countryside biogeography is challenged by the imperative to move beyond a descriptive science, to one that can predict the distributions of species in human landscapes into the future. This goal can be partially addressed through concentrating on population dynamics rather than snapshots of community structure. Ultimately, we need to know whether the populations we see in agricultural habitats in the countryside are self-sustaining, or whether they heavily rely on immigration from remnant patches of native habitat, be they small fragments or large formally protected areas. Further, when and under what conditions might countryside habitats act as population sinks or evolutionary traps, which lure migrants to their deaths thereby jeopardizing conservation within reserves? Finally, what is the relative strength of extinction debt and colonization credit in human-altered landscapes? Addressing these questions will be a challenge, given the data requirements involved [168]. To ascertain whether habitats (either natural or anthropogenic) are sinks, population vital rates (recruitment and mortality) and movements (emigration and immigration) must be tracked. For a single species, this requires long-term mark-recapture studies, with sufficient spatial sampling to quantify movement rates. Genetic studies tracking relatedness between populations in the countryside and more natural habitat are another option. However, for the biodiverse communities of concern in countryside landscapes, single-species approaches are unlikely to grant much insight into the community as a whole, given the diversity of ways that organisms respond to environmental gradients in the countryside. Unfortunately, short cuts, such as using multi-season dynamic occupancy models to examine extinction-

colonization dynamics of entire populations, do not offer a clear solution. Pernicious population sinks can remain continuously occupied through immigration, even as individuals experience heightened mortality or diminished reproductive rates. The collection of community-wide datasets of population trajectories at the landscape scale are therefore a challenging, but necessary, target for research.

(iv) *Evolutionary history of countryside species*

A surprising number of species use and even seem to specialize on primarily open agricultural habitats in the countryside. For example, a recent synthesis reported that approximately 10% of birds, 30% of reptiles, and 35% amphibians were found exclusively in open agricultural habitats and not in reserves within the Coto Brus landscape of Costa Rica [8]. These rates of unique species occurring in human-dominated habitats or rates of abundance increases in human-dominated habitats are consistent with other studies [111, 169]. Given that anthropogenic habitats are evolutionarily novel, where did these species come from? Potential hypotheses include that these species evolved to exploit tropical forest gaps, evolved in open grassland or scrubland habitat in nearby biological zones, or evolved in forests, but are coincidentally (pre-) adapted to agriculture under certain climate conditions. This last point is supported by the observation that lowland forest species preferentially occur in open countryside habitats in mid and upper elevations, where climates are cooler and more analogous to shaded lowland forests [114, 115]. In addition to contemporary studies of habitat affiliations across broad climate gradients, a promising path to address the evolutionary origin of countryside species may be through phylogenetic analysis. For example, one hypothesis is that clades of countryside species underwent heightened evolutionary diversification or experienced lower extinction risk during periods in Earth's history when grassland predominated.

Conclusion

The discipline of countryside biogeography has documented a sizeable fraction of landscape-scale biodiversity residing within human modified-countryside habitats [4, 8]. Only by seeking to understand the complete distribution of organisms, in protected reserves, in heavily altered ecosystems, and everything in between, will it be possible to tailor conservation practices that preserve diversity across entire regions. As noted above, improving the conservation value of countryside habitats may not benefit many threatened, forest-restricted species. Thus, intensifying agriculture and sparing land natural states may maximize total biodiversity preservation in some situations [170, 171]. Ultimately, however, the future of biodiversity conservation will likely necessitate both formal

protected areas and wildlife-friendly agriculture and other human-modified land use types. Taking an explicitly inclusive view of biodiversity across the countryside forces the recognition of the intrinsic and extrinsic value of the species that co-inhabit the human realm. This inclusive view allows researchers to shed light on longstanding scientific questions regarding the distributions of species, address how humanity has altered these distributions, and ultimately point towards win-win strategies to conserve nature alongside a burgeoning human population.

Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

Human and Animal Rights and Informed Consent This article does not contain any studies with human or animal subjects performed by any of the authors.

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