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# How should beta-diversity inform biodiversity conservation?

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# Abstract

To design robust protected area networks, accurately measure species losses, or understand the processes that maintain species diversity, conservation science must consider the organization of biodiversity in space. Central is beta-diversity—the component of regional diversity that accumulates from compositional differences between local species assemblages. We review how beta-diversity is impacted by human activities, including farming, selective-logging, urbanisation, species invasions, overhunting, and climate change. Beta-diversity increases, decreases or remains unchanged by these impacts, depending on the balance of processes that cause species composition to become more different (biotic heterogenization) or more similar (biotic homogenization) between sites. While maintaining high beta-diversity is not always a desirable conservation outcome, understanding beta-diversity is essential for protecting regional diversity and can directly assist conservation planning.

**Key words:** biodiversity conservation; biotic homogenization; alpha-diversity; beta-diversity; gamma-diversity; diversity partitioning; pairwise dissimilarities; species-area relationships; spatial scaling

### Conservation targets at multiple spatial scales

As we enter the Anthropocene, humankind is reorganizing the biosphere [1]. Processes ranging from overhunting of large-bodied vertebrates [2] and moving alien species across biogeographic barriers [3] to wholesale clearing of natural habitats for agriculture [4] continue to erode biodiversity. Society values biodiversity at multiple spatial scales, with concerns ranging from local provision of ecosystem services [5] to global preservation of the intrinsic and instrumental value of species [6]. For example, the United Nations Convention on Biological Diversity seeks to stem biodiversity loss at regional, national, and global levels [7].

To assess how best to conserve biodiversity across spatial scales, we need to understand the relationship between locally-collected monitoring data and regional diversity dynamics, and how the mechanisms that maintain diversity vary from local to regional spatial scales [8-11]. Conservationists thus face a key question: how do changes measured locally scale up to regional impacts [12]?

The solution lies in our understanding of "beta-diversity"—the component of regional biodiversity ("gamma-diversity"; see Glossary) that accumulates due to inter-site differences between local species assemblages ("alpha-diversity"; Glossary) [13]. Measured appropriately, changes in beta-diversity provide the scaling factor that allows us to predict changes in gamma-diversity from measured changes in alpha-diversity. Furthermore, new techniques can shed light on the mechanisms responsible for beta-diversity maintenance from alpha-scale survey data, thereby revealing not only how biodiversity is organized in space [14-16], but also the mechanistic underpinnings of these patterns [9,17-19]. Such techniques provide conservation-relevant insights about the maintenance of diversity over large areas.

Conservation scientists can incorporate beta-diversity into management decision-making in a variety of ways. Studies of beta-diversity can quantify biodiversity loss [20] and inform the placement of protected areas [21,22], the management of biological invasions [23], and the design of wildlife-friendly landscapes [24-27]. However, the existence of many different metrics for beta-diversity, each suited to subtly different questions, has been a source of confusion and debate in the ecological literature (Box 1) [13,28-30].

If beta-diversity is to reliably aid conservationists, it is crucial that we define and measure it appropriately. We must carefully match appropriate metrics to specific problems, and judiciously choose spatial scales to measure local and regional patterns. At its best, beta-diversity is a clarifying concept that unifies conservation science across spatial scales. But at its worst, it can be a mathematical abstraction that is easy to misapply and misinterpret. In this review, we highlight recent advances and potential pitfalls in the application of beta-diversity to conservation science.

## Using beta-diversity for conservation: metrics, opportunities, and pitfalls

### *Diversity loss and spatial scaling*

Conservation planning requires detailed biodiversity data to inform actions ranging from land purchases and management [31-33] to agricultural policy and international carbon payments [34-36]. However, our understanding of the magnitude of biodiversity loss (or gain) depends on the scale at which we measure it [37]. For example, local-scale patterns often suggest that diversity is maintained [38,39], whereas global-scale patterns indicate that we are in the midst of an unprecedented extinction event [40,41]. Scale-dependent differences in diversity maintenance can even be apparent even within single landscapes or study sites [20,23]. Therefore, we must understand biodiversity loss at spatial scales relevant to conservation goals.

Carefully interpreted metrics of beta-diversity can help to meet this challenge by revealing the scaling relationship between alpha- and gamma-diversity. Diversity partitioning beta-diversity metrics (Box 1) directly provide the scaling factors that relate alpha- and gamma-diversity, but their calculation requires prior knowledge of gamma-diversity. Pairwise dissimilarity measures (Box 1) are more widely applicable, but they convey unreliable information about these scaling relationships [42]. Null model approaches, which are widely used to remove the neutral component of beta-diversity, tend obscure the scaling relationship between local and regional diversity [43](Box 2). However, new techniques using the distance-decay of pairwise similarity provide a potentially powerful tool for extrapolating small studies to larger landscapes [44](Box 3).

Even when the scaling factor is measured appropriately, the conservation significance of a change in beta-diversity is not straightforward. Maximizing beta-diversity is not necessarily desirable for gamma-diversity conservation, because damaging anthropogenic impacts can cause the similarity of local communities to increase, decrease, or remain unchanged, depending on the relative balance of homogenization and heterogenization processes at the site level (Figure 1). During the initial stages of anthropogenic impacts, localized species losses and invader establishment might cause beta-diversity to increase (Figure 1b). Even when beta-diversity decreases, compensatory changes in alpha-diversity can buffer gamma-diversity against declines in beta-diversity (Figure 1a; [45]). For example, increases in the site-occupancy of rare species cause beta-diversity to decline, but bode well for gamma-diversity conservation. Furthermore, different beta-diversity metrics can change in opposite directions in response to a single disturbance event [13]. Therefore, any measured changes in beta-diversity must be interpreted with care.

### *Identifying mechanisms of diversity maintenance*

Null model controls and pairwise beta-diversity metrics (Box 1, Box 2) provide mechanistic insight about the maintenance of gamma-diversity, allowing the development of landscape-specific conservation actions (e.g. designing protected area networks). Null model controls can help us partition beta diversity between the component expected by chance (neutral sampling effects) and that driven by environmental or dispersal filters [9,43]. Such distinctions may help guide management, but even 'neutral' beta diversity may be of conservation interest (Box 2). Pairwise dissimilarities can identify key spatial or environmental gradients where turnover occurs [8,18,46], and analysis of pairwise dissimilarities before and after disturbance could pinpoint the environmental gradients along which beta-diversity has been lost, thereby directing the preservation or restoration of key features. By calculating multiple metrics, studies can arrive at a more general understanding of how beta-diversity responds to disturbance (Box 4). A growing body of literature has begun the task of applying these various metrics to assess human impacts on beta-diversity, but it remains critical to recognize what each metric emphasises.

## How humans have impacted beta-diversity

When human impacts are patchy in space, beta-diversity is likely to increase at the landscape scale [47,48]. However, human activities often generate completely novel landscapes, with unpredictable changes to alpha-, beta-, and gamma-diversity. Here, we review the beta-diversity impacts of five globally ubiquitous conservation issues. Our primary goal is to extract rules of thumb for interpreting alpha-scale studies of human disturbance. However, patterns of beta-diversity differ not only between disturbance types, but also among taxa and geographic locations. In some cases, patterns of beta-diversity are well established, with clear mechanistic underpinnings, but in many cases patterns are seemingly idiosyncratic or contradictory, without obvious mechanistic explanations. Where rules are not apparent, we advise caution in interpreting the implications of alpha-scale studies for landscape- or regional-scale biodiversity. These areas are frontiers for additional research.

### *Farming, tree plantations, and selective logging*

Intensive pasture and mechanized agriculture usually erode beta-diversity compared to natural habitats and wildlife-friendly agriculture, as the spatially uniform conditions within intensive farmland are tolerable to only a small subset of abundant native species [24,25,49]. For example, Japanese larch plantations have homogeneous leaf-litter compared to natural forests, and thus lower beta-diversity among litter-dwelling invertebrates [50]. In European farms, pesticide-use decreases multiplicative beta-diversity for many invertebrate taxonomic groups [51] (but see [25]). Reductions in beta-diversity can persist following cessation of agriculture due to species filtering based on dispersal ability. Understory plant communities regenerating on abandoned agricultural land tend to have reduced beta-diversity because they are dominated by dispersal-adapted species compared to ancient controls [26].

When high-intensity land use reduces the total abundance of the many species across the assemblage, beta-diversity can increase as species become rarer (Fig. 1), even though species-environment relationships tend to weaken (Box 4)[20]. This increase is identified by null model controls as being driven by neutral sampling effects of rarity (Fig. 1b). Conversely, when land use intensification leads to high abundances and local richness of a particular group (e.g. hoverflies in Europe [44], bees and wasps in Ecuador [52]), beta-diversity is likely to decline.

Although there are some clear generalities, many changes appear idiosyncratic. For example, forest clearance homogenizes soil bacteria and decreases bacterial beta-diversity in the Brazilian Amazon, but has the opposite effect in Borneo [53,54]. In Europe, plants and spiders show opposite trends (increasing and decreasing beta-diversity, respectively) across conventional and organic wheat fields in Europe [25], while in Borneo, bacteria and birds show different trends following logging (increases and minimal change, respectively) [33,54]. In Egypt, gardening increases plant heterogeneity compared to natural habitats by introducing novel crop species, but pollinator heterogeneity remains unchanged [55]. These findings reflect marked variability in the scaling and processes of diversity maintenance between regions and taxonomic groups. Further research is needed to better understand how and why these differences arise.

### *Urbanisation*

Urbanization consistently reduces between-city beta-diversity, compounding severe declines in alpha-diversity [56,57]. Among birds, urbanization decreases the distance decay of compositional similarity between cities [58,59]. In insects, urbanization reduces beta-diversity because heterogeneous assemblages of specialists disappear from cities, while consistent suites of tolerant species persist. For example, in Switzerland diverse assemblages of birch-specialist true bugs and leafhoppers show high turnover in rural areas, but are absent from cities [60]. In southern California, urbanization increases soil moisture, which permits the establishment of an invasive ant that homogenizes native ant communities by excluding all but a few species [61].

Native plant assemblages tend to become more homogeneous with urbanization [62], and cities often support numerous invasive species, which tend to have lower turnover than natives [63]. Recently established exotics, however, can show higher beta-diversity than natives [62,64], suggesting a short-term heterogenizing process prior to the more widespread establishment of invasives (Figure 1).

Despite ubiquitous declines in beta-diversity between cities, there is a more complicated pattern within cities. Distance decay in Australian birds is high among both the most urbanized and least urbanized neighbourhoods, but is lower at intermediate levels of urbanization [59]. Similarly within Berlin, 100 $m^2$ tree plots in the most and least urbanized areas are more dissimilar than intermediately urbanized plots [65]. Effects like these may account for why, among European birds, urban species-area relationships are as steep as rural relationships [58].

*Biological invasions*

Biological invasions affect diversity in two ways: by adding non-native species and by excluding natives. Both processes can initially heterogenize communities as the invader spreads, but can ultimately result in biotic homogenization once the invader is ubiquitous (additive homogenization due to the invader's ubiquity, and subtractive homogenization if natives are extirpated; figure 1)[63,64,66]. Conservationists are mainly concerned with minimizing the impacts of invasives on native species, rather than maximizing the total diversity of invaded communities (i.e. including both invasives and natives), so the subtractive processes are of primary interest. We consider two important cases where the impacts of invasive species can depend on spatial scale: competition effects, exemplified by plant invasions; and predator-prey effects, exemplified by predator introductions on oceanic islands.

Although the presence of exotic plants can increase alpha-diversity [67], plant invasions often decrease the diversity of *natives*, at least over small spatial extents [3]. However, few plant extinctions are attributable to competition from invaders [68], and recent work suggests that they do not generally drive declines in gamma-diversity, even of natives [23,69]. Extensive plant surveys from Great Britain suggest that invasives are not causing island-wide extinctions [69]. Targeted surveys of heavily invaded sites from the United States (Florida, Missouri, and Hawaii) reveal that invasive plants sharply reduce diversity at very fine spatial scales (1$m^2$ quadrats), but not at moderate scales (500$m^2$ plots; figure 2) [23]. Thus, where invasive plants reduce native diversity at local scales, beta-diversity tends to increase and gamma-diversity is maintained (but see [70]).

Unlike introductions of invasive plants, the introduction of rats, cats and other predators on oceanic islands has decimated both alpha- and gamma-diversity of island species [71]. The catastrophic loss of avian diversity in the Pacific, where as many as 2000 species have disappeared since the arrival of man [72], precipitated a huge decline in beta-diversity, because island-adapted endemic species were disproportionately likely to go extinct, whereas insular populations of widespread species typically retained better defences to invasive predators [71]. Among nonpasserine birds, wide-ranging species were 24 times more likely to persist on islands than single-island endemics, causing the subtractive homogenization of island communities across large scales [73].

*Hunting and fishing*

Scant information is available about the impact of hunting and fishing (exploitation) on beta-diversity. Exploitation often targets large-bodied species, and these tend to range widely. Thus, exploitation may magnify local differences in species assemblages and increase beta-diversity. For instance, fishing in the northwest Atlantic targets large-bodied species and increases the decay of community similarity with distance, an undesirable process of subtractive heterogenization [74]. Exploitation also has indirect effects on beta-diversity. For example, bottom-trawling homogenizes benthic communities by destroying microhabitats on the sea floor [75]. In tropical forests, hunting removes seed dispersers, causing hyperdiverse tree assemblages to give way to depauperate communities of species capable of recruiting near conspecific adults [76]. This subset of trees is likely to be replicated across space, leading to declines in beta- and gamma-diversity [11].

*Climate change*

Rapid climate change is already causing dramatic shifts in eco-climatic conditions, threatening species diversity globally [77]. Although community turnover is often organized along climatic gradients [78], few studies have asked how climate change affects beta-diversity. Available evidence suggests that recent climate change has increased beta-diversity in some systems by decreasing local richness, without driving regional extinctions. For example, in California's Sierra Nevada, climate change has yet to cause regional extinctions of birds or mammals, but has caused ubiquitous declines in local richness, increasing the neutral component of beta-diversity [79,80]. The long-term effects of climate change on turnover remain to be seen. Species differ widely in their capacity to track shifting climate envelopes, depending in part on their dispersal capacity [81], suggesting that future communities may be dominated by more dispersive taxa. Alongside predicted climate-driven declines in specialists [77], this could result in increasing homogenization of communities with ongoing climate change, in both natural and anthropogenic landscapes.

## Applications to conservation management

By revealing the spatial scaling of diversity loss and the mechanistic underpinnings of diversity maintenance, beta-diversity has much to offer conservation science. Here, we discuss the application of beta-diversity to specific longstanding problems in conservation management.

*Protected area selection*

Given that conservation is underfunded, protected area selection is an exercise of optimisation [82]. Landscape patterns of beta-diversity have obvious implications for the SLOSS debate (is it better to create a Single Large Or Several Small reserves?)[83]. In landscapes with high species turnover along spatial or environmental gradients, protected area networks must successfully capture this variation or risk losing species [84]. Thus, turnover might favour multiple spatially disjunct reserves over single large parks [22,85,86]. On the other hand, high neutral beta diversity or nestedness (richness differences along spatial gradients) imply that conservation could better focus on diverse sites at the expense of species-poor areas.

When null models suggest that turnover results primarily from neutral processes in a well-mixed community, conservation should maximize the total area protected, with less emphasis on protected areas' geographic locations. For example, only large protected area networks will encompass a full complement of tropical forest trees, even in well-connected tracts of environmentally homogeneous forest [11].

### *Corridors and dispersal facilitation*

Habitat fragmentation can increase beta diversity via dispersal limitation and neutral processes [87]. Such patterns may indicate a need to increase between-patch connectivity via corridor creation [88]. Successful corridors might decrease beta-diversity, at least in the short term, by allowing better mixing between patches. However, corridor creation is likely to benefit all forms of biodiversity in the long term, by reducing the likelihood that local and regional extinction debts are realized [88].

Corridors could also facilitate species range-shifts in response to climate change [81]. These shifts tend to follow poleward and upward temperature shifts in terrestrial biomes, and downward shifts in aquatic biomes, although all species within a community will not necessarily shift in the same direction [89,90]. Species differ markedly in rates of climate-driven movement, reflecting variation in dispersal capacity and phenotypic plasticity [81]. Creating habitat corridors along climate gradients is likely to aid the movement of poor dispersers, reducing the potential homogenizing effect of climate change. In the short term, such corridors may still decrease beta-diversity by facilitating mixing between currently isolated communities, but the long-term effect is likely to be positive due to avoided extinctions. Because species respond to multiple climatic factors including temperature and precipitation, identifying the environmental determinants of species' range limits can help us optimize the location and orientation of such corridors [18,91].

### *Land-sharing versus land-sparing agriculture*

Agriculture is a major driver of the global extinction crisis [4]. Strategies for minimizing biodiversity impacts range from implementing low-yielding wildlife-friendly practices over large areas (land-sharing) to promoting intensification whilst saving natural habitat for conservation (land-sparing). Quantitative studies of biodiversity loss can reveal the relative merits of the two approaches [34]. However, most studies have focused on much smaller spatial extents than the regional biota that they seek to conserve. Encouragingly, the few studies that have looked at beta-diversity in a land-sparing versus land-sharing context have largely found that alpha-scale conclusions are unchanged [27,92]. Classically, land-sharing and land-sparing are compared on the basis of population changes across species, rather than species richness [34]. Therefore, conclusions depend more heavily on whether compositional change is subtractive or additive than on whether it is homogenizing or heterogenizing (Figure 1). The loss of specialist species in low-intensity agriculture is likely to simultaneously favour land-sparing and to drive subtractive homogenization [20,35].

Beta-diversity carries two additional implications for the land-sharing versus land-sparing debate. First, land-sharing is inherently farm-based, whereas intensification on one farm can theoretically spare land at disparate locations. Therefore, the homogenizing effects of farm intensification under land-sparing could be counterbalanced if spared areas are located in an area where beta-diversity is higher or more prone to homogenization. Second, uniformity of agricultural practices and policies over large areas is inherently likely to reduce beta-diversity at coarse scales. This might even be true for agri-environmental management, if the same management practices are applied across large areas, and those practices favour a particular suite of species. A heterogeneous landscape that includes agri-environmental management as well as natural habitat and high-intensity agriculture (land-sparing) might better maintain alpha-, beta- and gamma-diversity at coarse scales, suggesting a need for land-use policy to incorporate diverse options and incentives.

## Concluding remarks and future directions

Much of what we know in conservation science comes from studies conducted in small areas. Detailed gamma-diversity data will likely never exist for most of the globe, especially at regional scales and in understudied remote tropical regions. Therefore, we need to better understand processes and patterns in the maintenance and loss of beta-diversity in order effectively conserve gamma-diversity [12]. We need to examine how beta-diversity responds during land-use change to understand when and how alpha-scale research can be scaled up to gamma-scale problems and how management interventions can improve gamma-diversity conservation. We cannot afford to abandon the insights gained from alpha-scale studies, but we must update these insights using knowledge about our impacts on species turnover. Recent basic and applied advances in the study of beta-diversity are a welcome beginning [9,20,26].

Current research priorities are myriad (Box 5). Expanding on existing analyses [15,16], we need to document baseline patterns of beta-diversity at increasingly fine resolution. We need a broader and deeper understanding of the effects of land-use and climate change on beta-diversity, sufficient to develop robust methods of extrapolation for interpreting alpha-scale studies. Doing so will require that numerous studies of human biodiversity impacts report consistent metrics for beta-diversity (e.g. ‘true’ beta-diversity). At the same time, we must identify imperilled natural processes that have historically maintained beta-diversity, and target management to ensure their ongoing operation.

Whereas alpha- and gamma-diversity insights have long underpinned both local-scale conservation actions and regional to global scale policy initiatives [7], the adoption of beta-diversity research into conservation remains a critical frontier. Conservation scientists need to better engage with policy-makers and practitioners to communicate what losses or gains of beta-diversity mean for the global biodiversity extinction crisis, and in turn, how those results should inform decision making. Contemporary threats and solutions in conservation occur at all spatial scales. Beta-diversity provides the link that integrates conservation insights across them all.

## Glossary

**Alpha-diversity** The species diversity of a relatively small area, frequently expressed as species richness or other low-order Hill number [29]. For the purposes of this review, alpha-diversity corresponds to the scales at which biodiversity studies commonly make measurements (i.e. diversity of a quadrat, plot, or study site).

**Beta-diversity** The component of gamma-diversity (see below) that accumulates as a result of differences between sites. Includes heterogeneity resulting from including stochastic variation within a single habitat, differences between habitats along environmental gradients, and changes in species composition between biogeographic provinces [13]. Unlike alpha- and gamma-diversity, beta-diversity does not correspond to the total diversity of some region of space. See box 1.

**Gamma-diversity** The species diversity of a relatively large area, expressed in the same units as alpha-diversity (see above). For the purposes of this review, gamma-diversity corresponds to the regional-to-global scales over which society wants to maintain biodiversity (i.e. diversity of a landscape, ecoregion, nation, or planet).

**Nestedness** The component of beta-diversity that reflects differences in alpha-diversity between sites when species assemblages at different sites are nested subsets of one another [93]. Contrasts with *turnover* (see below).

**Neutral sampling** The random assortment of species into samples, either due to sampling errors (e.g. random failure to detect species in a sample) or due to random community assembly in nature.

**Similarity (also Compositional similarity)** A metric of how similar the species assemblages of two (or more) sites are. Numerous similarity metrics each define a different formulation of compositional similarity (see box 1).

**Turnover** The component of beta-diversity that reflects the replacement of species at some sites by different species at other sites [93]. Contrasts with *nestedness* (see above).

**BOX 1: Measuring beta-diversity for conservation science**

The literature contains numerous beta-diversity metrics [13,29]. All relate to compositional heterogeneity, but they have subtly distinct biological meanings and conservation significance.

*Diversity partitioning*
*True beta-diversity* (the ratio gamma-diversity divided by mean alpha-diversity) partitions gamma-diversity into multiplicative alpha and beta components [29,94] (Figure I). Likewise, *additive beta-diversity* partitions gamma into additive components [21,95]. These exact partitions are ideal for revealing the spatial scaling of diversity loss, but they can only be used if gamma diversity is known.

*Pairwise dissimilarities*
Various indices quantify compositional dissimilarity between pairs of sites [28]. *Pairwise beta-diversity* is the average dissimilarity across all such pairs within a region [13] (Figure I). In addition to yielding summary metrics for beta-diversity, the pairwise dissimilarities are useful for identifying environmental or geographic features that structure beta-diversity, since the magnitude of the compositional dissimilarity between two sites should correlate with between-site differences in these features [13].

The choice of dissimilarity metric has been widely discussed [28], but rarely in a conservation context. While abundance-based measures [30] depend less on sample size than presence-absence measures, they achieve this precisely by giving less weight to rare species. Thus, presence-absence measures might be most appropriate for biodiversity conservation geared towards rare species (despite their sample size dependence), while abundance-based measures might be preferred in analyses of ecosystem service provision, which is dominated by common species. $\beta_{sim}$ [28] is a widely recommended presence-absence measure that is nearly as insensitive to sample size as the best abundance-based measures, and measures only turnover (not nestedness; see below). For these reasons, it is especially apt for identifying spatial and environmental gradients where rare-species turnover occurs, when sampling is sparse or uneven.

*Turnover and nestedness*
Whether measuring beta-diversity using diversity-partitioning or using pairwise dissimilarities, ecologists often distinguish between two patterns of beta-diversity termed *turnover* and *nestedness* [93]. Turnover occurs when species present at one site are absent at another site, but are replaced by other species absent from the first. Nestedness occurs when species present at one site are absent at another, but are not replaced by additional species. Turnover across natural sites implies that conservation must target multiple sites, while nestedness suggests that conservation might target the richest sites.

**Box 1, Fig I**

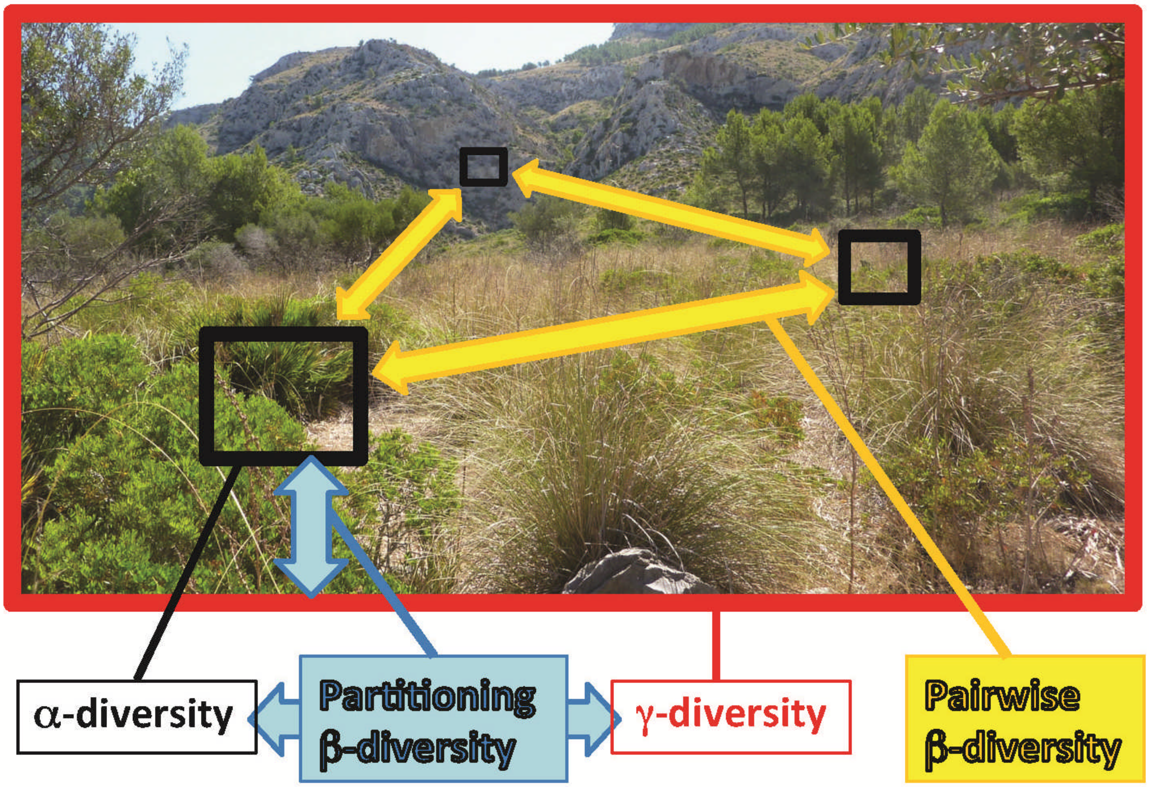

**Figure I.** When local sites harbour different species, beta-diversity can be calculated either by comparing the average alpha-diversity to the total gamma-diversity (diversity partitioning), or by assessing pairwise dissimilarities between local sites.

## BOX 2: Null models for beta-diversity

Even in homogeneous communities, sampling effects can lead to heterogeneity among sites [9]. Rare species will typically be absent from some local samples, and samples from a species-rich assemblage will contain different subsets of the assemblage, even if the community is well mixed. Whenever gamma-diversity exceeds alpha-diversity, these neutral sampling effects ensure that the average pairwise dissimilarity between sites is nonzero, even if species sort randomly into sites.

Null models are available to distinguish neutral sampling effects from beta-diversity that exists due to ecological mechanisms such as dispersal limitation or environmental filtering [9,99,100]. Null models randomly reshuffle species identities among the local biodiversity samples, generating a null expectation for beta-diversity under a random assembly process that controls for alpha- and gamma-diversity. These models are important when using beta-diversity to infer mechanisms of community assembly, because they calculate the amount of beta-diversity attributable purely to neutral assembly processes [43]. Frequently, this null expectation is subtracted from the observed beta-diversity metrics as a correction to remove the neutral sampling effects.

While null models are highly useful for distinguishing mechanisms of community assembly, they are not helpful for understanding the scaling relationship between the local samples and gamma-diversity. To do so, it is crucial to include scaling that results from neutral assembly processes. Some incidence-based null models fully control for the difference between alpha- and gamma-diversity [99], and therefore cannot yield meaningful estimates of the scaling relationship between the two.

Abundance-based null models also obscure the scaling relationship. To illustrate, consider a forest with 20 ubiquitous common species and 20 rare species. A typical tree plot contains 19-20 of the common species, but only 1-2 rare species. Plots differ due to sampling effects driven by the rare species. If every rare species goes extinct, plot-scale diversity changes by only 5-10%, but gamma-diversity is halved. The null model correctly concludes that only the null component of beta-diversity has changed—yet this component matters crucially to the scaling relationship.

## Box 3: Upscaling biodiversity

Regional-scale conservation decisions often rely on estimates of gamma-diversity that are extrapolated from a sparse set of local biodiversity samples. Prominent techniques for estimating gamma-diversity assume that local samples are independently drawn from a single regional community [96], but within-region dispersal limitation or environmental filtering violate this assumption. Therefore, measurements of beta-diversity are important for understanding the spatial scaling of species richness.

Traditional pairwise methods do not automatically yield estimates of gamma-diversity or the spatial scaling between alpha and gamma, because they fail to account for patterns of co-occurrence among more than two sites [42]. Recently Hui and McGeoch [97] proposed a new method, generalising beta-diversity to examine overlap in trios, quartets, and larger collections of samples. “Zeta-diversity” ($\zeta_i$ ) describes the species shared by any collection of *i* samples, such that $\zeta_1$ is the average richness of a singe sample, $\zeta_2$ is the average number of species shared by pairs of samples, $\zeta_3$ is the average shared by trios, and so on. Zeta inevitably declines with *i*, but the functional form of this decline may vary (most frequently either as power-law or exponential). This approach effectively constructs a “collector’s curve” of increasing sample number, and allows it to be partitioned into the contribution of successively higher levels of overlap. However, unless one has an exhaustive set of samples covering the whole region of interest, one can only assess gamma-diversity by extrapolation.

A different approach is to take advantage of the rich spatial information contained in pairwise dissimilarites to directly estimate gamma-diversity (and indeed the full species-area relationship). This can be done for specific idealised models of community structure [98], but until recently no general formulation was available. Azaele et al. [44] use a general pair correlation function (PCF) to empirically fit the spatial turnover of species as a function of distance (Figure I). The technique has so far been tested in a limited number of systems, but represents an important general approach for multi-scale biodiversity monitoring. Initial tests on well-studied forest plot data suggest this offers a useful new approach to link the beta-diversity of local samples to the gamma-diversity of the region from which they are drawn. The approach can be adapted to incorporate virtually any species-abundance distribution or PCF, or to incorporate environmental as well as spatial distances. Such extensions should provide a new and powerful toolbox for investigating beta-diversity and spatial scaling.

**Box 3, Fig. I**

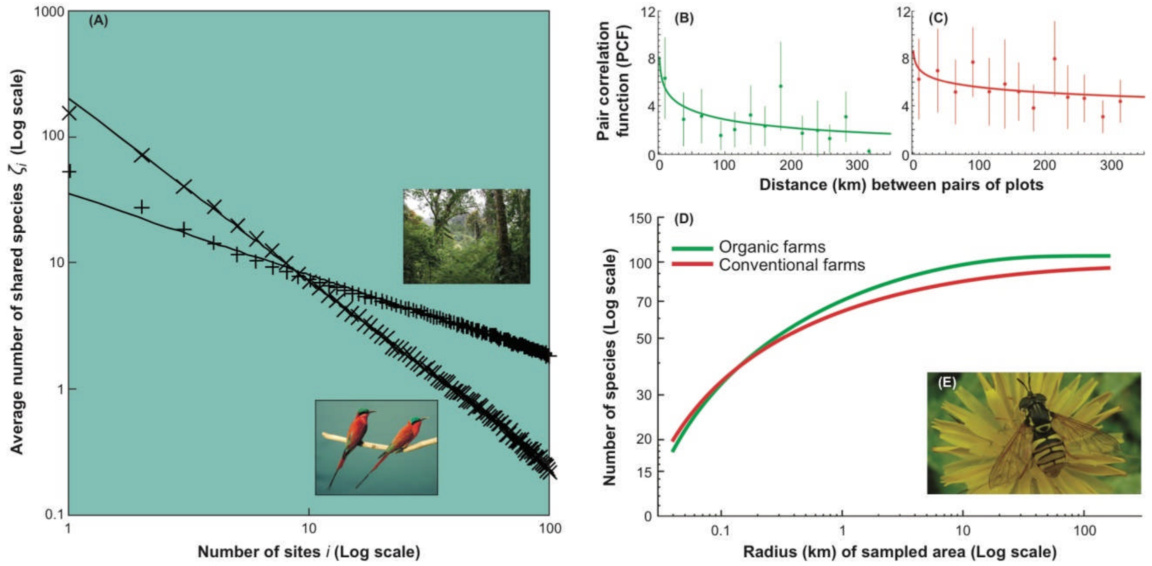

**Figure I. (A)** Power-law zeta-diversity ($\zeta_i$) curves for trees sampled by 20 x 20 m quadrats on Barro Colorado Island, Panama (+), and birds sampled in quarter-degree cells in southern Africa (X) [97]. Zeta-diversity describes higher order overlaps between sites, but has not been used as a tool for inferring gamma-diversity. **(B,C)** The similarity of hoverfly assemblages in England decays more rapidly with distance on organic farms **(B)** than on conventional farms **(C)**, and this is reflected in the respective pair correlation functions (PCF). Dots represent empirical PCF (±1SD) and curves are best-fitted curves. **(D)** As a consequence, the upscaled species-area relationships inferred by Azaele et al. [44] cross; thus while organic farms have fewer species in a local sample, they are predicted to have more species at landscape-scales larger than ~4 hectares. **(E)** Conventional farms are dominated by highly mobile species with larvae that feed on cereal aphids, while organic farms exhibit a large fraction species belonging to other feeding guilds that show higher turnover, such as this *Chrysotoxum sp*. Data figures from [97] (A) and [44] (B-D) and photograph reprinted with permission from William Kunin.

## Box 4: Multiple beta-diversity metrics in Costa Rican agriculture

Low-intensity agriculture in Costa Rica supports local bird communities that are nearly as diverse as forest, but intensification erodes this diversity [35]. To better balance farming and nature in tropical countryside, it is important to understand how agriculture impacts beta-diversity. Karp et al [20] used multiple beta-diversity metrics to understand how beta-diversity changes across three land-use categories: forest, low-intensity agriculture (LIA), and high-intensity agriculture (HIA; Figure I).

Countervailing the decline in alpha-diversity, both pairwise beta-diversity and true beta-diversity are slightly higher in LIA than forest, and substantially higher in HIA. Additive beta-diversity (from data in [35]) reveals a similar picture, except that forest and LIA are indistinguishable, with HIA much higher. Thus, disturbance impacts gamma-diversity much less than alpha-diversity.

However, pairwise dissimilarities contain additional information. When Karp et al examined pairs of sites from environmentally disparate areas, HIA had significantly lower dissimilarities (i.e. higher beta-diversity) than either forest or LIA. Regressing pairwise dissimilarities on geographic distance between sites revealed that the similarity decreased with distance more rapidly in forest and LIA than HIA. Thus, HIA did not appear to maintain the compositional difference between disparate locations as well as other land uses.

Seeking to explain HIA's very high beta-diversity, Karp et al. noticed that total bird abundances were very low in these habitats. Thus, they implemented a null model control to calculate the expected beta diversity if birds sorted randomly into local samples. They found that this neutral sorting accounted for a large portion of HIA beta-diversity, a sizeable portion of LIA beta-diversity, and a much lower portion of forest beta-diversity. "Null" beta-diversity was therefore maintaining gamma-diversity in agricultural habitats, even as bird communities were driven to low total abundance.

What are we to conclude from these disparate patterns? First, because the scaling factor from alpha to gamma-diversity is by far highest in HIA, gamma-diversity consequences of intensification could be less dire than alpha-scale measurements might suggest (although gamma consequences may be time-lagged due to extinction debt). Second, intensification homogenizes bird diversity at large spatial scales, which bodes ill for the prospects for tropical diversity in massive swaths of high-intensity agriculture. Third, HIA (and to a lesser extent LIA) maintain high beta-diversity largely through neutral sampling effects and not through species-environment relationships, which could indicate trouble for habitat specialists. Finally, multiple measures of beta-diversity paint a fuller picture of change than any single metric.

**Box 4, Fig I**

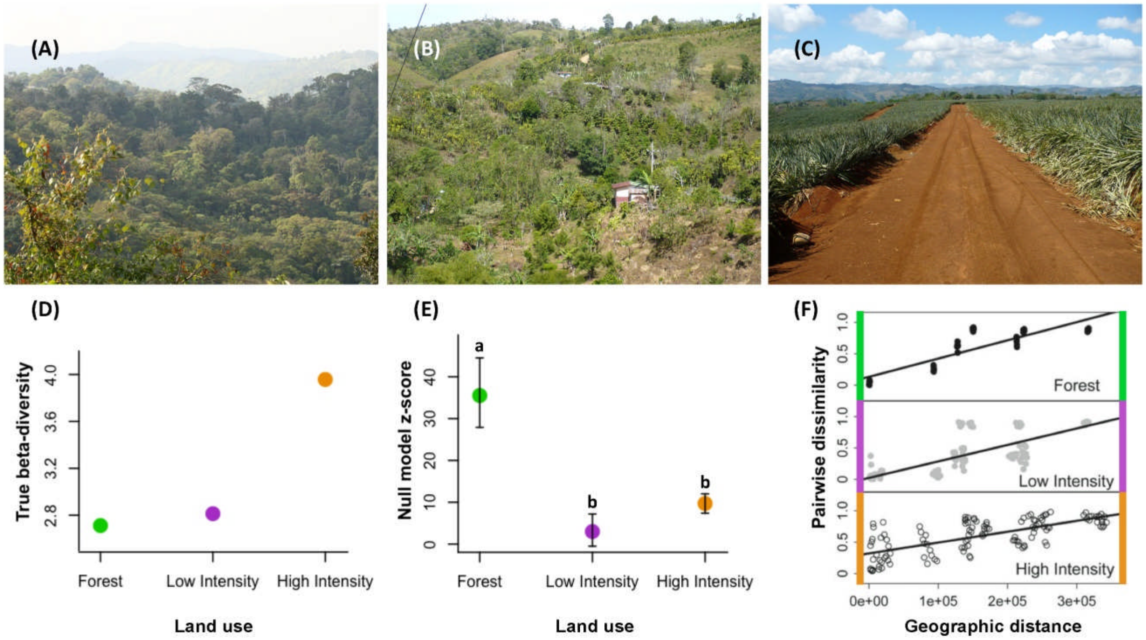

**Figure I**. Impacts of farming in Costa Rica on beta-diversity. **(A)** Natural forest, **(B)** low-intensity agriculture, and **(C)** high-intensity agriculture studied by Karp et al. **(D)** Point estimates of true beta-diversity show very high beta-diversity in high-intensity agriculture. **(E)** Null model controls reveal that much of the beta-diversity in high-intensity agriculture is due to neutral sampling effects. **(F)** The distance decay of similarity is lowest in high-intensity agriculture, so distant agricultural sites are more similar to each other than are distant forest sites from each other. Photos courtesy of D. Karp and J. Zook; data figures from [20], reprinted with permission from John Wiley and Sons.

## Box 5: Outstanding questions

### ***Research questions***

*Upscaling from samples to gamma-diversity:* The estimation of gamma-diversity from a set of samples is a complicated problem, and even more so when spatial structure means that samples are not independent. A novel approach offers substantial promise [44] (Box 3), but has yet to be repeatedly tested and improved. Modifying the framework to include environmental distances between sites and geographic barriers is a frontier, and validating the framework's predictions will be a key challenge.

*Developing rules of thumb:* As yet, we cannot say with confidence how beta-diversity is likely to respond to most human activities (urbanization is a notable exception), although experience to date suggests that the effects may depend critically on the extent (in space and time) of the modification. Rules of thumb based on replicated empirical studies reporting standard beta-diversity metrics would allow conservation to qualitatively extrapolate alpha-scale data to larger regions, even when quantitative upscaling is not possible. This could have far-reaching consequences for contemporary questions such as the land-sharing versus land-sparing debate.

### ***Data gaps***

*Taxa:* The available data on how beta-diversity responds to human impacts is biased towards plants and birds. Since other organisms have dramatically different modes and patterns of dispersal, we must better understand how their beta-diversity is changing in the Anthropocene.

*Systems*: Studies of beta-diversity are biased towards terrestrial systems in temperate and tropical latitudes. Very little information is available regarding beta-diversity change in aquatic systems, and essentially no reports have assessed the effect of anthropogenic change on beta-diversity at high latitudes, which generally show less natural beta-diversity (i.e., in the absence of human impacts) than at lower latitudes [15].

*Disturbances:* While the beta-diversity consequences of farming and invasions are comparatively well studied, the literature contains very little on the consequences of climate change and hunting, and even less on myriad other disturbances ranging from surface pollution to alternative energy development. Even for a specific mode of disturbance, the spatial pattern and extent of disturbance might further influence beta-diversity.

*Replication*: Even in relatively data-rich taxa, systems, and disturbances, we so far lack the replication of results necessary to separate signal from noise and build rules of thumb. We suggest that almost any biodiversity study that incorporates land-use could beneficially calculate and report beta-diversity metrics, thus contributing to an emerging understanding of biodiversity loss across spatial scales.

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## Figures

### Figure 1

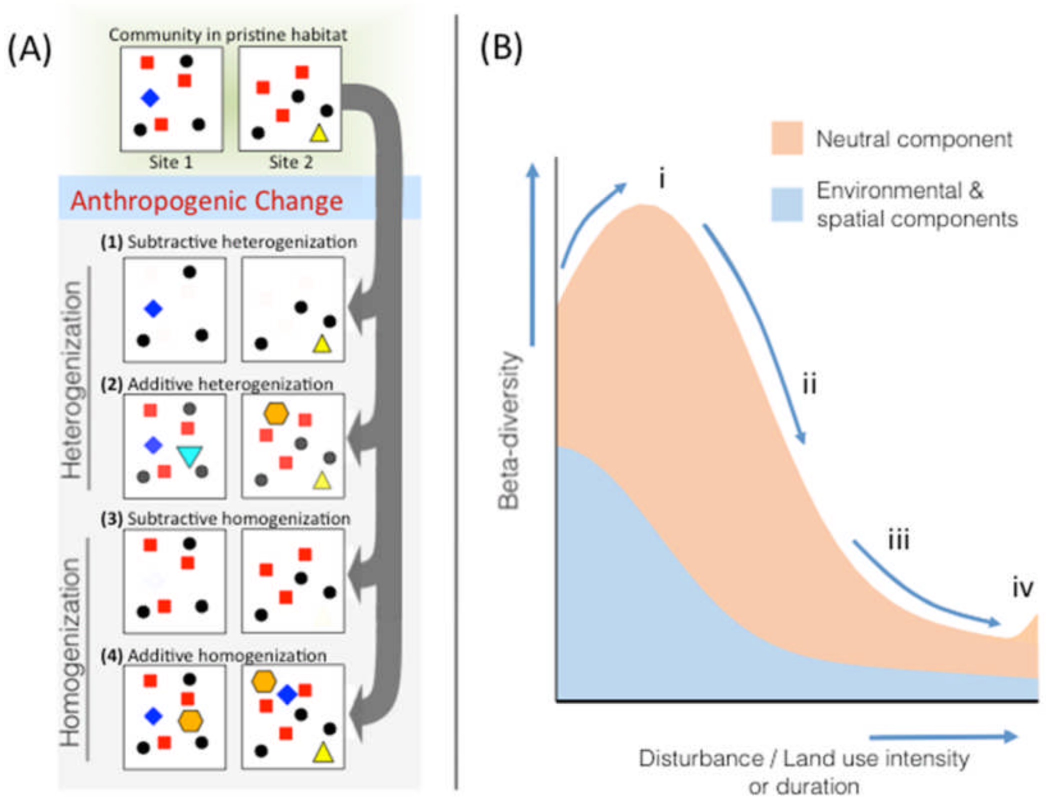

**Figure 1:** Beta-diversity can change in a variety of ways following human impacts. **(A)** Beta-diversity can change as a result of local species gains (additive processes) and local species losses (subtractive processes). Beta-diversity increases when ubiquitous species disappear from some or all sites (1) or when new species arrive at some sites, but do not become ubiquitous (2). Beta-diversity decreases when rare, non-ubiquitous species go extinct (3) or when formerly rare or absent species become widespread (4). **(B)** A conceptual trajectory for typical patterns of beta-diversity change as human disturbance persists and intensifies. (i) Many native species become rarer, but few go extinct (subtractive heterogenization). Invasive species establish, but few become ubiquitous (additive heterogenization). (ii) Rare species disappear entirely (subtractive homogenization); generalists and invaders begin to dominate (additive homogenization). (iii) Homogeneous environments with little between-site variation. (iv) If assemblages are driven to very low abundance, the neutral component of beta-diversity may again increase.

**Figure 2**

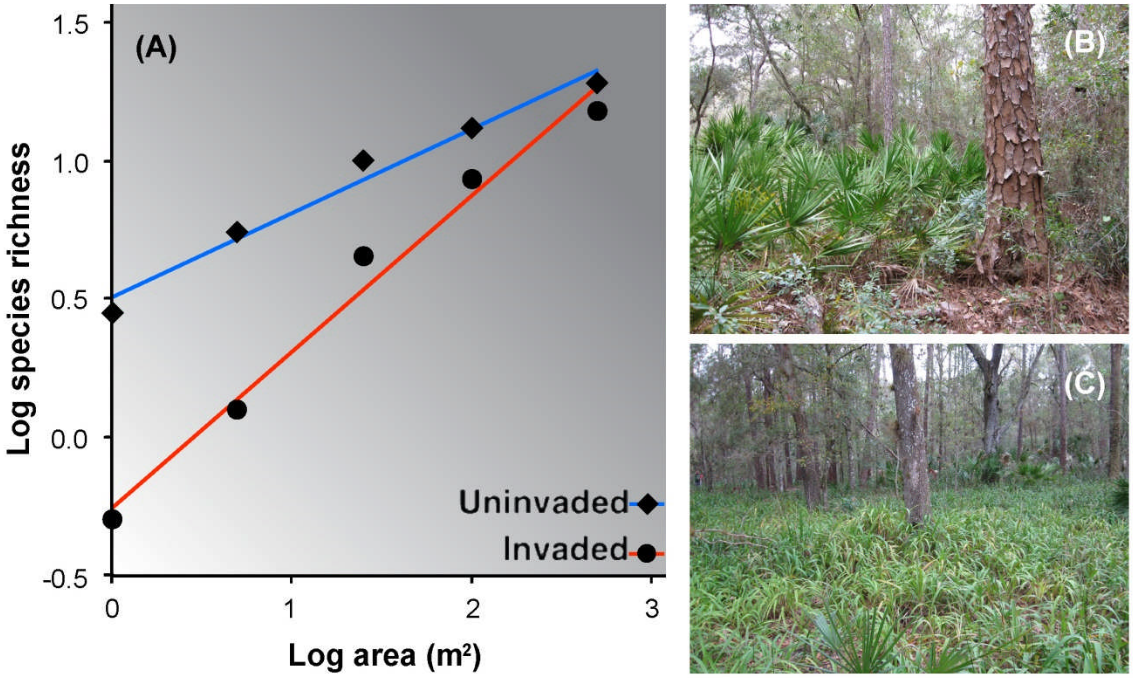

**Figure 2: (A)** An example species-area relationship from hardwood hammocks in Florida, USA. Uninvaded sites (**B**) have shallower slopes than sites invaded by *Dianella ensifolia* (**C**). At larger sample areas, the number of species between uninvaded and invaded sites converges. Photos courtesy of K. Powell. Panel **(A)** from [23]. Reprinted with permission from AAAS.