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PERSPECTIVE

Realigning the land-sharing/land-sparing debate to match conservation needs: considering diversity scales and land-use history

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Abstract The "land sharing versus land sparing" concept provides a framework for comparing potential land use patterns in terms of trade-offs between biodiversity conservation and agricultural yields at a landscape scale. Here, we raise two additional aspects to be considered in the sparing/sharing debate, supported by a review of available literature. First, beta and gamma (instead of alpha) diversity measures capture landscape scale variance in biodiversity in response to land use changes and should be considered for the long-term management of agricultural landscapes. Moreover, beta and gamma diversity may better account for comparisons of biodiversity between spared and shared land use options. Second, land use history has a pronounced influence on the complexity and variance in agricultural habitat niches at a landscape scale, which in turn may determine the relevance of sparing or sharing land use options. Appropriate and comparable biodiversity metrics and the recognition of landscape history are two vital preconditions in aligning biological conservation goals with maximized yields within the sparing/sharing framework.

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Introduction

The current land sharing versus land sparing debate in conservation biology seeks to balance agricultural production and biodiversity conservation based on the analysis of trade-offs between agricultural yield and biodiversity conservation. Within this debate, the land use patterns span a continuum from (1) land sharing, which aims to maintain biodiversity within spatially more heterogeneous and less intensely used agricultural landscapes (Fischer et al. 2008), to (2) land sparing, which attempts maximizing agricultural yields within a fixed extent, thereby allowing potential agricultural land to be set aside as biodiversity reserves (Balmford and Bond 2005; Phalan et al. 2011a). Arguments supporting both sparing and sharing management strategies are manifold (Fischer et al. 2011; Tscharntke et al. 2012a; Gabriel et al. 2013; Ramankutty and Rhemtulla 2013) and the conceptual framework—for brevity henceforth referred to as “sparing/sharing”—has generated considerable debate within conservation biology, land use science and related fields.

Here, we propose that two key concepts, beta/gamma diversity relations and land use histories, may aid in (1) realigning sparing/sharing research to conservation management scales and (2) identifying the types of landscape under which sparing or sharing are most likely to be successful strategies for balancing agricultural production and biodiversity conservation. We consider diversity relations and land use history in the context of the empirical, landscape scale peer-reviewed sparing/sharing literature and the main management recommendation of such studies.

Based on a review of the available literature we identified 96 publications relevant for the discussion, 21 of which were empirical landscape/regional scale studies (Table 1), where biodiversity was quantified. The majority of the remaining publications were discussion, review or perspective papers ($n = 50$), with a smaller number of model simulations ($n = 10$). The remaining 15 publications either had a global focus or no quantification of biodiversity (see appendix 1 for details).

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Alpha, beta and gamma diversity

The sparing/sharing framework has an explicit focus on landscape-scale analyses where it considers the trade-offs between biodiversity conservation and agricultural yield mediated via land use management. This requires careful consideration of the diversity metrics that are most appropriate to address trade-offs between yield and biodiversity at the landscape scale. Based on our review, almost 62 % ($n = 13$) of empirical sparing/sharing research to date relied on plot and field based sampling, often for single taxa groups (62 % of studies), to extrapolate biodiversity–yield relations across broader landscape extents (see Table 1 for an overview of the empirical studies). However, in order to be able to extrapolate biodiversity–yield relations across broader scales (e.g. landscapes or regions) the spatial resolution at which landscape patterns are quantified needs to match the resolution at which the sparing/sharing framework is applied, including relevant scales of policy intervention (e.g. regional, national, EU-scale). Furthermore, it is crucial to recognize that different taxa may respond to changing land use configurations (and related ecological processes) very differently across landscape scales (Foreman 1995). Deriving conclusions regarding sparing/sharing options from plot or field based focal habitats, or single taxa, regarding the effects of landscape scale land use strategies may be misleading. We therefore propose that a focus on beta or gamma diversity is required when analyzing the landscape effects of different land use options within the sparing/sharing continuum.

The increase in species richness within a plot (alpha-diversity) for a given land use strategy may not be related to changes in total species richness (gamma-diversity) across the whole landscape (e.g. Gabriel et al. 2006; Egan and Mortensen 2012). Agricultural landscapes are often characterized by heterogeneous and complex land use patterns. When focusing on a plot scale in such landscapes, the variance in species diversity may be greater between study plots (within one landscape) than the variance between landscapes

Table 1 Review of studies focussing on the land sharing/land sparing nexus, defining the system the study was conducted in, the species groups being in the focus of the study, and the biodiversity metric used (examining a species-area relationship, was interpreted as an approximation beta diversity)

Study	Dominant landscape	Agricultural frontier	Biodiversity measured	Biodiversity metric	Proposed solution
Blanco and Waltert (2013)	Tropical	Yes	Chimpanses	Species abundance (alpha)	Sparing
Chandler et al. (2013)	Forest	Yes	Bird	Alpha and communities	Sparing
Clough et al. (2011)	Tropical	Yes	Plants, fungi, vertebrates, invertebrates	Species richness (alpha)	Sharing
Edwards et al. (2014)	Forests	Yes	Birds, beetles, ants	Alpha	Sparing
Edwards et al. (2010)	Tropical	Yes	Birds	Species richness (alpha)	Sparing
Egan and Mortensen (2012)	Agricultural systems	No	Vascular plants	Species richness, species area relationships (beta)	Sharing in complex landscape, otherwise sparing
Gabriel et al. (2006)	Agricultural landscapes	No	Vascular plants, earthworms, arthropods, butterflies, birds	Abundance and species densities (alpha)	Mixed
Hodgson et al. (2010)	Agricultural landscapes	No	Butterflies	Population density, species richness (alpha)	Sparing for intensive and sharing for extensive lanndscapes
Hulme et al. (2013)	Coffee plantations	Yes	Birds	Population density (alpha)	Sparing
Lentini et al. (2012)	Woodland	No	Bats, arthropods	Occurence (alpha)	Mixed
Macchi et al. (2013)	Argentina dry forest	Yes	Bird communities	Indices and community patterns (beta)	Sparing
Mahood et al. (2012)	Amazon	Yes	Birds	Species richness (gamma)	Sparing
Maskell et al. (2013)	Agricultural landscapes	No	Plants and ecosystem services	Species diversity (gamma)	Scale dependant
Phalan et al. (2011a)	Ghana and India	Yes	Birds and trees	Species densities (alpha)	Sparing
Phalan et al. (2011b)	Ghana and India	Yes	Trees and birds	Population densities (beta)	Sparing
Pywell et al. (2012)	Temperate	No	Birds, bumbelbees, plants	Beta	Sharing
Quinn et al. (2012)	Great plains	No	Birds	Abundance (alpha)	Both, scale dependant
Quinn et al. (2013)	Woodland and grassland	No	Birds	Occurence (alpha)	Sharing
Sheldon and Styring (2011)	Tree plantations	Yes	Birds	Species richness, diversity and species accumulation curves (gamma)	Sparing
Steffan-Dewenter et al. (2007)	Forest	Yes	Plants, insects, soil arthropods	Alpha and beta	Sparing

Table 1 continued

Study	Dominant landscape	Agricultural frontier	Biodiversity measured	Biodiversity metric	Proposed solution
Wade et al. (2010)	Forest	Yes	Trees	Species richness (alpha)	Yield dependant

Studies were detected using a Scopus, ISI and scholar google search, which yielded a total of 96 studies, out of which all empirical studies were included in our analysis. For a complete list of all studies examined see appendix S1

due to local dynamics, gradients and disturbance (Tscharntke et al. 2012b). Agricultural landscapes may therefore have relatively high beta diversity due to alpha diversity patterns that fluctuate in response to individual habitat associations of different taxa and heterogeneity of the landscape composition. We argue that the use of alpha-diversity is hence particularly problematic for direct comparisons between biodiversity within spared landscapes (typically with lower within-landscape variance) and shared landscapes (typically with high within-landscape variance). Beta-diversity may better illustrate such changes in diversity linked to changes in land use configurations at boarder spatial scales than alpha-diversity (Egan and Mortensen 2012) and may allow for improved comparability between sparing and sharing options on a landscape scale (e.g. Gabriel et al. 2006; Egan and Mortensen 2012). A number of recent publications derived their conclusions based on the regional demographic condition of the species pool by assessing population densities (Hodgson et al. 2010; Phalan et al. 2011b; Hulme et al. 2013) or species accumulation curves/species area relationships (Sheldon and Styring 2011; Egan and Mortensen 2012). Complexity is added to the discussion by the composition of the landscape. Many agricultural areas are located in rather heterogeneous landscapes and biodiversity–yield interactions are typically more complex in such heterogeneous landscapes (Grau et al. 2013). This is often closely related with the scale of the given studies, and consequently many accounts arrive at scale-dependent effects when proposing management strategies, most notably in traditional agricultural landscapes (e.g. Egan and Mortensen 2012; Lentini et al. 2012; Quinn et al. 2012; Maskell et al. 2013). The potential scale mismatch and related sampling bias between diversity sampling and sparing/sharing analysis scales may be confounded by the variability in beta-diversity occurring in different habitat/landscape types (Egan and Mortensen 2012; Tscharntke et al. 2012b).

While beta-diversity allows for a better comparison between spared/shared landscapes e.g. due to a lower bias through sampling design and density, data on gamma-diversity would indicate lasting, long-term changes in diversity at a landscape level, across the sparing/sharing land use continuum. Loss of gamma-diversity due to a particular land use management option would ultimately lead to the permanent loss of traits, complex interactions and ultimately ecosystem functions. We argue that although alpha-diversity measured on a plot provides an understanding of the impact of different management options at the plot scale, an understanding of changes in beta- or gamma-diversity is more relevant from a conservation perspective (Gabriel et al. 2006; Tscharntke et al. 2012b) within sparing/sharing studies. We acknowledge that the sampling efforts for assessing beta/gamma-diversity are comparably high, yet they are necessary to allow for sound comparisons in trade-offs between biodiversity and yields under sparing and sharing options at the landscape scale.

Land use history

Both beta- and gamma-diversity are fundamentally influenced by land use history. Considering historic land use change can broaden our understanding of current species diversity patterns at landscape scales. Studies spanning the historical agricultural areas of Europe, Asia (Ranganathan et al. 2008) and the Americas (Ellis et al. 2013), have shown that agricultural landscapes established centuries ago continue to influence current land use schemes, species diversity (Lindborg and Eriksson 2004) and local species pools (Zobel et al. 2011). Historical land-use patterns show a strong influence on current species pools of arable weed species (Baessler and Klotz 2006) and even pre-historical agricultural practices continue to influence abiotic soil properties in arid ecosystems (Hall et al.

2013). We argue that land use history is a key factor that determines the choice between land sharing and land sparing strategies in current land use management. While it has been stated that for tropical regions land sparing strategies, and for temperate regions land sharing strategies might be the most appropriate (Ramankutty and Rhemtulla 2012), we propose that land use history is of key influence in the sharing/sparing debate, and should not be confused with a dichotomous difference between tropical and temperate landscapes. Instead we suggest that the difference between "frontier landscapes"—where primary habitat is under pressure from agricultural expansion—and traditional agricultural landscapes is of vital importance when considering sharing/sparing management recommendations. The legacy of land-use history for both ecological dynamics and conservation is well known on a landscape scale (Foster et al. 2002).

Where human induced land use changes allowed species to adapt, gamma-diversity may be altered, perhaps even increased, due to increased landscape heterogeneity and modified structure (Keil et al. 2012). For example, while some species will have been lost in the conversion of native habitats to agricultural landscapes, many species have found new ecological niches—often restricted to specific landscape structures, e.g. river banks or meadows (Maurer et al. 2006). In such traditional agricultural landscapes, the heterogeneity of landscape structures is key to biodiversity conservation (Benton et al. 2003). We define traditional agricultural landscapes as areas where land cover modification by humans has created a patchy cultural landscape over a long enough time period (Lindborg and Eriksson 2004) to allow for the majority of species to shift and adapt their niche at a landscape level (Vos and Meekes 1999). Agricultural intensification in traditional agricultural landscapes often involves removal of the landscape structures, such as field margins in which the majority of the biodiversity resides (Schuch et al. 2012). In this context land sparing via intensification of parts of the landscape is likely to have a detrimental impact on biodiversity, particularly given that conservation of current biodiversity on the "spared" land has to involve maintaining the traditional agricultural practices that created the heterogeneous landscapes and that support the current gamma-diversity patterns. In traditional agricultural landscapes, the effectiveness of land sparing strategies are likely to be determined in a large part by the levels of agricultural intensification possible without loss of landscape structures. While there are surprisingly few empirical sparing/sharing studies in traditional agricultural landscapes none of the eight studies we identified solely supported land sparing. Whilst two studies endorsed land sharing (Pywell et al. 2012; Quinn et al. 2013), the other studies all underlined the importance of scale effects when considering land management (Hodgson et al. 2010; Egan and Mortensen 2012; Navarro and Pereira 2012; Quinn et al. 2012; Gabriel et al. 2013; Maskell et al. 2013).

In contrast to traditional agricultural landscapes, species are distributed more evenly in less disturbed and more uniform habitats such as intact forests and other "frontier landscapes". Thus increasing yield—via conversion of limited areas to agricultural production—potentially triggers a less drastic depletion of beta/gamma diversity. In such landscapes, the intensity of the agricultural production is likely to be less important than the total extent of area converted in terms of biodiversity loss. Given that sparing options require less land conversion for a given yield at the landscape scale it seems likely that sparing options will be preferable in relatively undisturbed systems (regardless if they are found in the tropics or not). In the empirical studies of sparing/sharing in frontier landscapes, 12 out of 13 studies endorsed land sparing strategies.

Consequences for conservation

Many traditional agricultural landscapes, such as the Mediterranean, are diversity hotspots, and their current rapid transformation threatens ecosystems and their diversity. In frontier landscapes (e.g. primary forests) intact habitats are rapidly converted into agricultural landscapes. In these rapidly transformed, often homogeneous frontier landscapes, diversity is depleted and cannot adapt to human induced changes. However, both intact natural habitats as well as traditional agricultural landscapes demand proper conservation schemes to foster a sustainable future, harmonizing the need for agricultural production with conservation of biodiversity and habitats. Using beta/gamma diversity may help to identify appropriate study scales, and would realign land sparing/sharing debates to the spatial scales appropriate for conservation management. A shared landscape might, for instance, show a higher habitat heterogeneity, which is

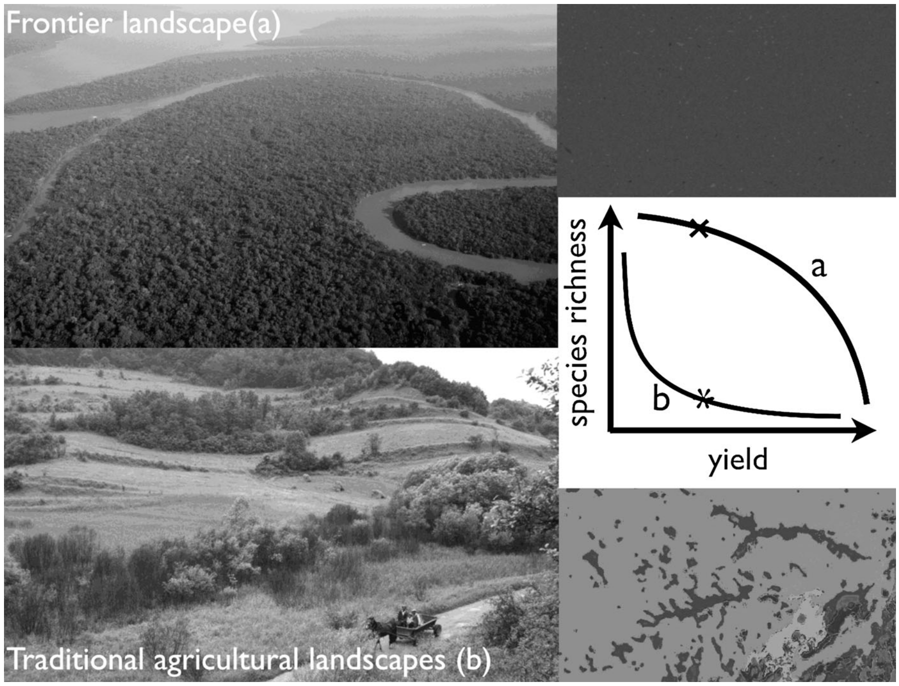

Fig. 1 Illustration of the relation between biodiversity and yield on a landscape scale. Both a frontier landscape (**a**) and a traditional agricultural landscape (**b**) can contain high biodiversity. Frontier landscapes are typically composed of primary intact regions that need to be conserved. There, intensification leads to loss of diversity, however, common species area relationships show that intensification of a proportion of the landscape (see the upper × in the graph) may results in a comparably small loss of total species richness. Consequently, many studies from frontier landscape encourage land sparing, yet there is no doubt that intact primary habitats need to be conserved, since many remaining primary frontier landscapes are today replaced by secondary landscapes. Traditional agricultural landscapes (**b**) contain much of the species richness in small areas, e.g. field margins, along rivers etc. Agricultural intensification (see the lower * in the graph) will often at first diminish these local richness hotspots, and sampling of species richness on a plot scale might underestimate habitats with high species richness; sampling should therefore consider heterogeneity and/or habitats types. The two schematic maps on the *right side* illustrate spatial biodiversity structure in the landscape, where (*a*) shows a rather evenly distributed high biodiversity shown in *dark grey*, while traditional agricultural landscapes (*b*) show a patchy and heterogeneous biodiversity, where highly diverse patches (*dark grey*) are distributed in a matrix of lower diversity (*light grey*), thus beta-diversity is comparably high. Photo **a** is licensed under creative commons (see appendix S2), photo **b** courtesy of Joern Fischer

why alpha diversity sampling would show higher fluctuations as compared to a spared landscape, where variance in alpha-diversity is widely driven by broad land use type or landscape composition (see Grau et al. 2013). As our review showed, more studies examining the sharing/sparing pattern across different landscape setting are needed to examine the trade-offs between biodiversity and yields, including sampling over multiple landscapes that have different composition and configuration. While the need to consider landscape heterogeneit, land use and species dynamics is recognised in landscape ecology and conservation biology, a wider embedding of these issues into the discussion on sharing/sparing is desirable. One might argue that studies focused on alpha-diversity are potentially biased towards supporting land sparing, and only studies with a high number of plots are likely to be able to grasp the complexity in biodiversity of shared landscapes (see Fig. 1). The sustainable development of landscapes demands consideration of its complexity (Wu 2013). Within traditional agricultural landscapes successful conservation strategies such as the UNESCO biosphere program that includes pronounced aspects of land sharing through integrated conservation are well established. On the other hand, intact primary forest should be protected (Pimm and Raven 2000). Thus, proposed future land use changes—via either sparing or sharing land use strategies—should be placed in the context of the speed and extent of previous land use changes as both, historic and future land use change, will determine the resulting diversity patterns.

Much is at stake in this heated debate, yet to date only some 21 empirical studies have explicitly assessed biodiversity at landscape scales under sparing and sharing option with the majority of these (13) focusing on frontier landscapes. More data is needed (Hayashi 2011), if generalizations are to be made, particularly given that the empirical studies to date show a considerable variance in terms of how biodiversity was measured, the taxa considered and landscape history of the study regions. More important, sample data has to be structured and collected in a way that relationships between beta-/gamma-diversity and productivity can be revealed and that considers land use history of the sites. It is also crucial that sampling designs, data analysis and interpretation are more carefully harmonized to allow meaningful comparisons between studies.

We therefore propose, following a long tradition in landscape ecology, that future studies should consider the characterization of landscapes based on the land use history and species diversity patterns. In the context of the land sparing/sharing debate considering spatial complexity mediated via appropriate diversity measures and land use history would increase comparability of the findings from different studies and provide more meaningful evidence for conservation management at the landscape scale.

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