

Harmonizing Biodiversity Conservation and Productivity in the Context of Increasing Demands on Landscapes

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Biodiversity conservation and agricultural production are often seen as mutually exclusive objectives. Strategies for reconciling them are intensely debated. We argue that harmonization between biodiversity conservation and crop production can be improved by increasing our understanding of the underlying relationships between them. We provide a general conceptual framework that links biodiversity and agricultural production through the separate relationships between land use and biodiversity and between land use and production. Hypothesized relationships are derived by synthesizing existing empirical and theoretical ecological knowledge. The framework suggests nonlinear relationships caused by the multifaceted impacts of land use (composition, configuration, and intensity). We propose solutions for overcoming the apparently dichotomous aims of maximizing either biodiversity conservation or agricultural production and suggest new hypotheses that emerge from our proposed framework.

Keywords: agricultural production, biodiversity conservation, land-use intensity, landscape configuration, landscape composition

Agrowing human population coupled with increasing per-capita consumption, changing diets, increasing food waste, and ineffective regulation have led to rising demands on ecosystems for the resources they supply (Foley et al. 2011, Tscharntke et al. 2012). Globally, there has been an increase in the amount of land cleared of natural vegetation (Seppelt et al. 2014), in the intensification of management activities (Pimentel et al. 2005), and in the simplification of landscape structure, such as through an increase in broadscale agricultural practices (Foley et al. 2005, van Asselen and Verburg 2012, Václavík et al. 2013). Suggestions have been made to design agronomic systems shifting from conventional to more closed, regenerative systems, which would reduce energy consumption and emissions (Pearson et al. 2007). However, as human land use and land transformation through agricultural systems currently pose the greatest threat to the world's terrestrial biodiversity (Pereira et al. 2010), there are significant scientific and societal challenges in recognizing and minimizing trade-offs between agricultural production and biodiversity conservation. There is growing (but uneven) political and societal

awareness that the protection of biodiversity in human-used landscapes is crucial, recognizing that human well-being is intimately linked with biodiversity via ecosystem services (Cunningham et al. 2013). In general, biodiversity attributes are positively linked with ecosystem services (e.g., Gamfeldt et al. 2013, Werling et al. 2014), but these relationships have been studied only for a limited set of ecosystem services (e.g., Thompson et al. 2011, Cardinale et al. 2012, Balvanera et al. 2014).

The Convention on Biological Diversity (CBD)'s definition of biodiversity as "the variability among living organisms from all sources including, *inter alia*, terrestrial, marine, and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species, and of ecosystems" allows for a wide variety of possible biodiversity metrics, such as species richness, functional diversity, phylogenetic diversity, or any kind of abundance–richness metrics, such as Simpson's diversity or Shannon diversity (Mace et al. 2012). Here, we focus on abundance–richness metrics because they account for abundance changes, which are likely to be important in

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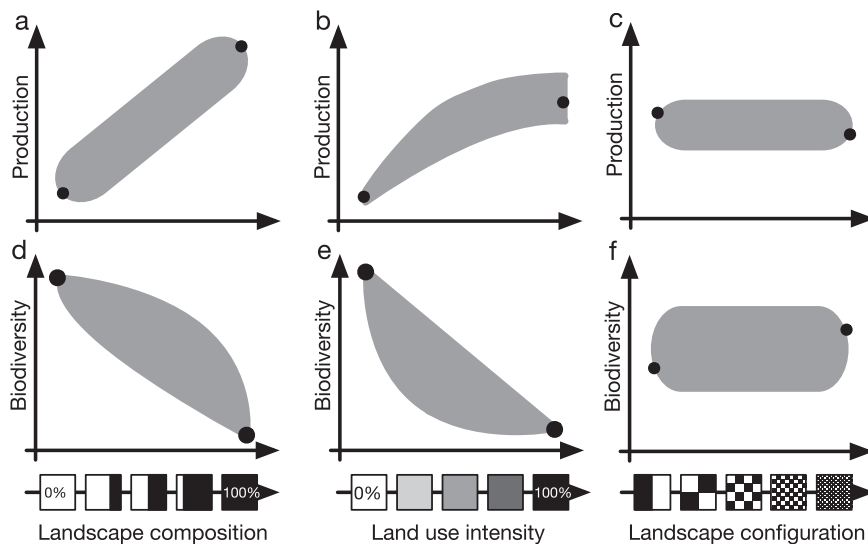


Figure 1. The foundation of the conceptual framework: hypothesized relationships of agricultural production (a–c) and biodiversity (measured with abundance–richness metrics; d–f) as a function of landscape composition (proportion of agricultural land), land-use intensity, and landscape configuration. Relationships represent a summary of current knowledge as reported in the published literature, with gray shading indicating uncertainty or lack of consensus. Black points illustrate the often-used dichotomous view, comparing just two levels of land use. In the depictions of land use, white coloring indicates areas of natural habitat, and gray or black coloring indicates areas of agriculture (with the intensity of gray indicating land-use intensity).

determining changes in ecosystem functioning and services (Cardinale et al. 2012) and are also less sensitive to the spatial scale of sampling than is species richness (Lande 1996, Chase and Knight 2013).

Although trade-offs between allocating land to production and biodiversity conservation have resulted in conflict and polarization (e.g., Tscharrntke et al. 2012), the scientific understanding of the underlying processes remains limited. Recently, there has been a debate about whether it is better to minimize agricultural impacts on biodiversity by separating the landscape into areas for the protection of biodiversity and areas of agriculture or by integrating biodiversity and production objectives in the same areas at the cost of optimal agricultural production (land sharing/sparing; Phalan et al. 2011, Fischer et al. 2014, von Wehrden et al. 2014).

These and other previous debates have presented an antagonistic set of land-use conditions in which human activities preclude the conservation of biodiversity. Studies that consider land-use gradients have frequently focused either on agricultural production or biodiversity, which limits our knowledge of how to mitigate trade-offs between food production and conservation. Therefore, there is an urgent need to develop a general, flexible, transferable framework that can be used for managing the trade-offs between agricultural production and biodiversity conservation, as well as global externalities resulting from the trade in agricultural products (Seppelt et al. 2011). Such a framework

would synthesize knowledge from many landscapes worldwide.

We propose such a framework and present some of the hypotheses that emerge from it. We begin by reviewing the current state of knowledge on the separate relationships between land use and agricultural production and between land use and biodiversity. We then synthesize these relationships into a framework for understanding the trade-offs between production and biodiversity. We argue that a complex and nonlinear relationship between biodiversity and agricultural production is likely, driven by nonlinear and context-dependent relationships between land use and production and between land use and biodiversity.

Land use–production relationships

Levels of agricultural production depend on a multitude of context-dependent factors, including land-use-management practices, land-use history, infrastructure, and access to markets and subsidies, many of which are correlated (Václavík et al. 2013). Human land use has led to a diversity of land systems worldwide that

differ widely in the amount of land dedicated to agriculture (i.e., landscape composition), the spatial arrangement of natural and agricultural elements in the landscape (i.e., landscape configuration), and the kind of management practices applied. The latter is most frequently understood as *land-use intensity*, characterized by the amount of inputs (chemicals, water, fertilizer, labor) and management aspects (stocking density, tillage regimes; van Asselen and Verburg 2012).

The most straightforward way to increase total production is by increasing the proportion of cultivated land in the landscape. Increased areas of arable land enable a near-linear increase in production (figure 1a), although once a certain threshold is reached, gains will be reduced by the inclusion of landscape patches less suited for agriculture and by the impairment of ecosystem functions arising from nearby natural habitat. Intensification is likely to lead to asymptotically increasing production, with diminishing returns (figure 1b) owing to limiting factors, such as radiation or water availability, or to the impairment of supporting and regulating ecosystem services, such as biocontrol or pollination (Kremen et al. 2007, Deguines et al. 2014). Overintensification might even result in a hump-shaped relationship if long-term processes, such as more frequent erosion events with loss of soil fertility, pest outbreaks due to lack of biocontrol species, or developing resistance against pest-control chemicals, are considered. This pattern of saturation is well known in agricultural economics and is usually

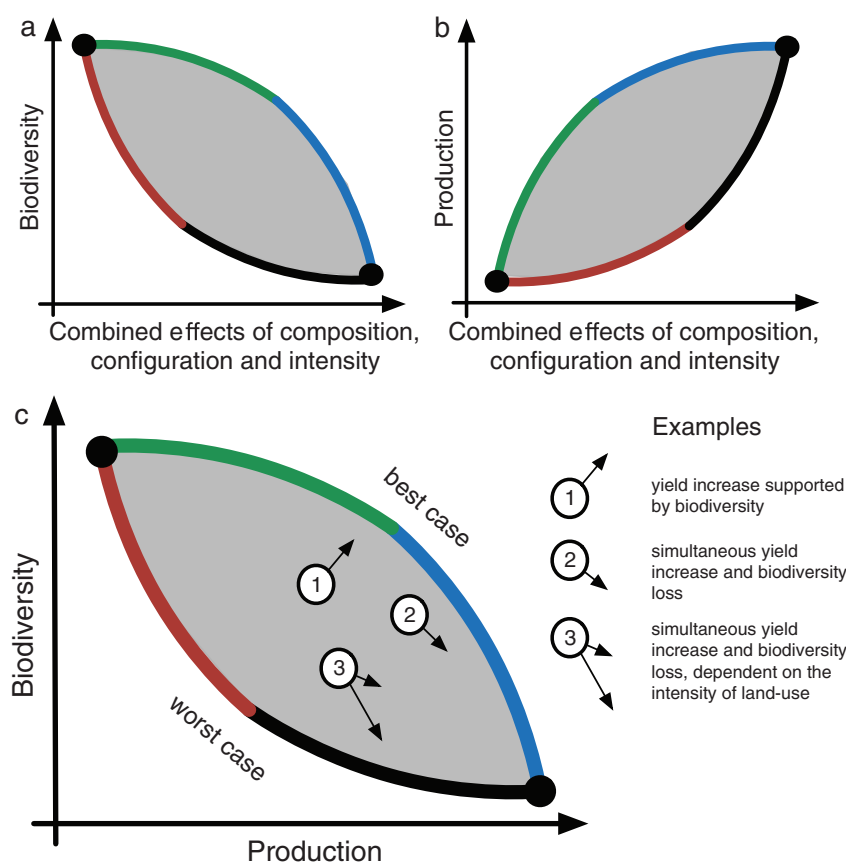


Figure 2. A synthesis of the conceptual framework: combining the relationships between land use and biodiversity (a) and between land use and agricultural production (b) leads to hypothesized relationships between agricultural production and biodiversity (c). In the top panels (a, b), we assume a combined effect of landscape composition, landscape configuration, and land-use intensity, with increased anthropogenic impact to the right. The colored arcs of the smaller upper panels translate directly to the arcs of the same color in the main panel and can be associated with different land-use systems. The shaded area in the main panel indicates the overall negative relationship between production and biodiversity, but different land-management options can lead to various relationships, as are indicated by the arrows within the shaded area: (1) an increase of both biodiversity and yield through species providing biocontrol (Finn et al. 2013); (2) loss of biodiversity through intensification (Storkey et al. 2011); and (3) different ratios of biodiversity loss and yield increase because of a difference in agricultural intensity (Donald et al. 2014); see the main text for full details.

referred to as a Cobb-Douglas function (Hayami 1970). Experimental studies could fully separate the effect of total area from intensity of use, but in real-world landscapes, we expect both aspects to interact.

The nature of the relationship between production and landscape configuration is less certain (figure 1c). There might be production benefits of larger farms with more continuous (i.e., less patchy) area under agriculture, owing to scaling effects or to increased management efficiency (Ihse 1995). There might also be production losses due to homogeneous management of large but heterogeneous fields.

However, higher production could be expected in more patchily farmed landscapes, owing to factors resulting from higher biodiversity and therefore better delivery of ecosystem services.

Land use–biodiversity relationships

Evidence strongly suggests that *biodiversity* (defined here as the combination of richness and abundance; see the introduction) decreases with an increasing proportion of agricultural land owing to the loss and fragmentation of natural habitats (figure 1d; Gerstner et al. 2014a, Newbold et al. 2014, 2015). The form of this relationship will depend on exactly how landscape composition affects the relative abundances of species: An accelerating loss of species is predicted by species-area relationships (Ladle and Whittaker 2011), although these generally assume—unrealistically—that agricultural land is entirely unsuitable for any species (Koh and Ghazoul 2010, but see Pereira and Daily 2006) and do not account for changes in abundance. However, if the majority of species are habitat specialists, a decelerating curve might be more likely with rapid initial losses.

In our framework, increasing land-use intensity can result in a decelerating decrease in biodiversity (figure 1e; as was shown by, e.g., Gerstner et al. 2014a). Small increases in intensity in minimally altered habitat initially lead to large losses of diversity, whereas further intensification will result in continuing but less dramatic declines (figure 1e; e.g., Kleijn et al. 2009).

Finally, the relationship between diversity and landscape configuration is uncertain, with various plausible relationships (figure 1f). Landscapes of simpler configuration might support a higher diversity if the remaining habitats are in larger patches (Gerstner et al. 2014a). However, landscapes of more complex configuration might support relatively high abundances of a greater number of species than simpler landscapes (Stein et al. 2014). Furthermore, small-scale extinctions in fragmented landscapes might be reversed through colonization if migration through the agricultural matrix is possible (Perfecto and Vandermeer 2008).

The available evidence suggests that landscape composition and, to a lesser extent, land-use intensity are the most important drivers of biodiversity (figure 1d and 1e; Fahrig

2013; Gerstner et al. 2014a, Newbold et al. 2015). However, landscape configuration may also be important (Benton et al. 2003, Gerstner et al. 2014a, Stein et al. 2014) and therefore needs to be considered in the proposed framework.

Synthesis: Land use and the biodiversity–production relationship

Figures 2a and 2b conceptualize the relationships discussed above leading to a range of plausible relationships between agricultural production and biodiversity. We show the combined effects of land-use composition, configuration, and intensity on a single axis, but this remains conceptual, and we do not attempt to define a combined metric. The colored arcs of the smaller upper panels translate directly to the arcs of the same color in the main panel and can be associated with different land-use systems. This ranges from best cases, in which biodiversity is both maintained within agricultural areas and supports production (upper edge of the gray shaded area in figure 2c), to worst cases, in which agricultural production is at the expense of biodiversity (lower edge of the gray shaded area).

High biodiversity and high agricultural production are possible where biodiversity can provide benefits to agricultural crops, such as through control of pests (Karp et al. 2013) or pollination (Deguines et al. 2014), and where agricultural areas are managed to maintain high levels of biodiversity (figure 2, green arcs). This requires specific management strategies such as intercropping, agroforestry, or provisioning of nesting habitats (e.g., for pollinators; Perfecto and Vandermeer 2008).

Tscharntke and colleagues (2005), for instance, showed that structurally complex landscapes compensate for local high-intensity management by enhancing local biodiversity. Kremen and colleagues (2007) provided a rationale for these relationships by proposing a model for mobile-agent-based ecosystem service, such as pollination or biocontrol. The functional relationship could be, for example, a hump-shaped curve (figure 2; Tscharntke et al. 2005), although quantitative data along such a complexity gradient are still lacking.

Beyond a certain point, only larger fields with more efficient production or more energy input and higher land-use intensity can achieve a further increase of production. Use of chemical inputs is increased, and practices that sterilize, structurally level, and standardize agricultural plots are promoted (Daily et al. 2003, Tscharntke et al. 2012). The consequences are rapid losses of biodiversity (Karp et al. 2012, Gerstner et al. 2014a) and comparably slower increases of agricultural yields (figure 2, blue arcs; Hayami 1970).

Where the focus is exclusively on agricultural production, biodiversity is lost quickly. In these cases, increasing production might be less successful if it depends on components of the biodiversity (figure 2, red arcs). This could lead to a worst-case condition for both biodiversity and production, characterized by antagonistic relationships between wildlife and agricultural production. For example, unsustainable

agricultural practices such as large-scale clearing of vulnerable soils may result in large losses of biodiversity but at the same time result in low and declining yields due to soil degradation (Sodhi et al. 2009). However, there are cases in which biodiversity under agricultural production is low and agricultural productivity can be achieved only through very high levels of intensification and degradation of the natural area (figure 2, black arcs). For example, this is the case for highly intense agriculture in the so-called Corn Belt of the US Midwest, with very high soil erosion, the depletion of aquifers, water pollution, the evolution of herbicide, and pesticide-resistant pests, etc. leading to a plateauing of agricultural production (Václavík et al. 2013).

Research capturing all three elements of the proposed framework is just emerging. By comparing monocultures with functionally diverse grassland systems at 31 sites in Europe, Finn and colleagues (2013) supported the hypothesis that more diverse landscapes can support higher agricultural yields and better maintain ecosystem function (in this case, resistance against invasion; figure 2c, example 1). Storkey and colleagues (2011) investigated the agricultural production–biodiversity relationship of arable systems in Europe, showing that higher yields are associated with a higher level of extinction threat among plant species (figure 2c, example 2). As floral diversity is still high in countries with modest inputs of agrochemicals, the authors assumed that land-use intensity is a major driver, although they acknowledged that countries with lower-intensity agriculture are also characterized by smaller field sizes and more complex landscapes. Storkey and colleagues (2011) therefore argued that establishing refugia on marginal land and field margins will play an important role for preserving threatened arable flora. Finally, Donald and colleagues (2014) showed that the populations of various farmland bird species declined in the twentieth century in Europe, with significantly steeper trends in countries with more intensive agriculture and higher cereal yields (figure 2c, example 3). Finally, using meta-analytic and synthetic review techniques, Letourneau and colleagues (2010) showed that pest-suppressive diversification schemes of landscapes interfered with production by reducing densities of the main crop, replacing it with intercrops or noncrop plants.

Conclusions

The proposed framework will help to identify key knowledge gaps and generates a number of hypotheses about trade-offs between agricultural production and biodiversity (box 1). Knowledge about the relationships among land use, biodiversity, and agricultural production is incomplete in several respects. Although previous studies focus on the species richness of plants, birds, and insects, which provide important ecosystem functions such as seed dispersal, pollination, and biocontrol, there is a lack of information on the relationships between species abundance and agricultural production. For example, it has been shown that the presence of weed patches in agricultural landscapes positively

Box 1. Hypotheses emerging from the conceptual framework.

Considering the effects of multiple aspects of land use (composition, configuration, intensity) on both agricultural production and biodiversity leads to novel hypotheses about the trade-offs between agricultural production and biodiversity conservation. The following list of hypotheses exemplifies the variety of research questions generated by the conceptual framework and may be extended, especially by considering more landscape contexts and species groups:

- (1) Landscape **configuration** affects agricultural production less compared with its impact on biodiversity. The difference of both effects is most pronounced in landscapes with intermediate proportions of agricultural land (**composition**).
- (2) Higher habitat diversity in the landscape (**configuration**) enhances agricultural production, because biodiversity and therefore the ecosystem functions that support production are supported by a larger number of edge habitats.
- (3) The higher the habitat diversity in the landscape (**configuration**), the stronger the impact of land-use intensification will be on biodiversity because of increasing exposure to edge habitats. This will result in land-use **intensification** being less effective in landscapes with higher habitat diversity, because the ecosystem functions supported by biodiversity will decrease more strongly.
- (4) The larger the fraction of land under agricultural production in the landscape (**composition**), the less effective land-use **intensification** will be for agricultural production (i.e., saturation in figure 1b appears earlier), because ecosystem functions supported by biodiversity are lacking.
- (5) Land-use **intensification** can compensate for reduced agricultural productivity caused by lower biodiversity; however, the marginal gain of agricultural production with increasing land-use intensity depends on the crop type(s) and the landscape composition and configuration.
- (6) Land-use **intensification** negatively affects biodiversity disproportionately more than it increases agricultural production—to different degrees depending on landscape **configuration** and **composition** and environmental conditions.

affects sunflower yields owing to higher visitation rates of bees and therefore more pollination (Carvalho et al. 2011). Previous studies have also been biased geographically (the examples discussed above focused on Europe). These studies do, however, illustrate how meta-analysis (Letourneau et al. 2010), large-scale field experiments (Finn et al. 2013), or analysis of secondary data (Storkey et al. 2011, Donald et al. 2014) can substantiate the framework by examining how land use moderates the relationship between biodiversity and agricultural production.

We have illustrated how various nonlinear relationships in the complex three-dimensional space of land use, biodiversity, and production could be conceptually synthesized into various relationships between production and biodiversity (figure 2). These relationships encompass the option space for reconciling biodiversity and production. Future research should aim to identify which relationships are seen in different situations. The framework goes beyond the dichotomous views taken in previous discussions, showing that a consideration of gradients in the different facets of land use allows an understanding of the nonlinear nature of the relationships. Moving away from a strictly dichotomous view is key to working toward a more complete understanding and more nuanced decisionmaking. A challenge remains to develop general metrics that combine all aspects of land use (configuration, composition, and intensity), which will allow the application of the proposed framework.

The proposed conceptual framework not only synthesizes the numerous possible nonlinear relationships known from theoretical and empirical studies but also provides guidance

for addressing information gaps by experimental studies or meta-analyses. Most of the available literature focuses on just two out of the three dimensions of land use, biodiversity, and production. Although these available studies have informed the framework, additional information is required to fill the missing dimensions, to elucidate the underlying mechanisms, and to identify those land systems that provide the smallest trade-offs or greatest synergies between biodiversity and agricultural production. It is therefore of high priority for ecologists studying land use–biodiversity relationships to also obtain estimates of agricultural production. We also encourage broadening the set of biodiversity indicators used to include species' abundance information.

Finally, the framework identifies possible options for reconciling demands for agricultural production with demands for biodiversity conservation. Although most studies arguing for sustainable land-use strategies have only addressed single dimensions of land-use change, a thorough study of the impacts of multiple alternative ways to increase production is necessary to identify, within a specific context, the most beneficial ways to balance biodiversity conservation and agricultural production. There are multiple unexplored combinations of landscape composition, configuration, and management, which might offer the opportunity to manage landscapes optimally both to feed the needs of a growing human population and to conserve biodiversity. Conservation of biodiversity needs to be achieved by designing appropriate production systems, which contain and benefit from higher biodiversity, rather than focusing only on the protection of pristine habitat.

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