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PERSPECTIVE

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Land-sharing/-sparing connectivity landscapes for ecosystem services and biodiversity conservation

Ingo Grass[1] | Jacqueline Loos[1,2] | Svenja Baensch[1,3] | Péter Batáry[1,4] | Felipe Librán-Embid[1] | Anoush Ficiciyan[1] | Felix Klaus[1] | Maraja Riechers[2] | Julia Rosa[1] | Julia Tiede[5] | Kristy Udy[1] | Catrin Westphal[1,3,6] | Annemarie Wurz[1] | Teja Tscharntke[1,6]

[1]University of Goettingen, Agroecology, Göttingen, Germany; [2]Leuphana University, Institute of Ecology, Lueneburg, Germany; [3]University of Goettingen, Functional Agrobiodiversity, Göttingen, Germany; [4]MTA ÖK Landscape and Conservation Ecology Research Group, Vácrátót, Hungary; [5]University of Muenster, Animal Ecology and Multitrophic Interactions, Institute of Landscape Ecology, Münster, Germany and [6]Centre of Biodiversity and Sustainable Land Use (CBL), University of Goettingen, Göttingen, Germany

Correspondence
Ingo Grass, Department of Crop Sciences, University of Goettingen, Agroecology, Göttingen, Germany.
Email: ingo.grass@agr.uni-goettingen.de

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Abstract

1. The land-sharing versus land-sparing debate recently stagnated, lacking an integrating perspective in agricultural landscapes as well as consideration of ecosystem services. Here, we argue that land-sharing (i.e. wildlife-friendly farming systems) and land-sparing (i.e. separation of high-yielding agriculture and natural habitats) are not mutually exclusive, as both are needed to balance management needs for the multifunctionality of agricultural landscapes.
2. Land-sharing promotes ecosystem services in agricultural settings, thereby allowing for environmentally friendly production. Land set aside in protected areas by land-sparing is crucial for conservation of those species that are incompatible with agriculture.
3. Importantly, as species move throughout the landscape and exploit different habitats, increased connectivity between environmentally friendly managed and protected areas is needed to (a) promote spillover of ecosystem service providers from land-sharing/-sparing measures to agricultural production and rescue service-providing species from extinction in hostile areas, (b) to facilitate immigration and counteract possible extinctions in spared habitats and (c) to conserve response diversity of species communities for ensuring resilience of ecosystem services in changing environments.
4. In conclusion, the successful management of multifunctional landscapes requires the combination of context-specific land-sharing and land-sparing measures within spatially well-connected landscape mosaics, resulting in land-sharing/-sparing connectivity landscapes.

KEYWORDS
agriculture, landscape design, landscape management, land-sharing, land-sparing, multifunctionality, sustainability

1 | INTRODUCTION

In times of FAO claims for higher crop production to feed the world and the current UN 'Decade of Biodiversity', agriculture increasingly collides with biodiversity conservation. In an often polarized debate, researchers and conservationists have been arguing for several years whether land-sharing (low-yield, environmentally friendly agriculture on a larger footprint of land) or land-sparing (high-yield, conventionally intensified agriculture on a smaller footprint of land) will reconcile agricultural production with biodiversity conservation (Bennett, 2017; Fischer et al., 2014; Green, Cornell, Scharlemann, & Balmford, 2005; Kremen, 2015; Phalan, Onial, Balmford, & Green, 2011) (Figure 1). With the debate primarily centring around agricultural production and biodiversity conservation, surprisingly little effort has been made to integrate the ecosystem services concept into the land-sharing/-sparing framework (Bennett, 2017). This lack of integration also pertains to ecosystem services that stem from biodiversity associated with agriculture, such as crop pollination or biological pest control. Given that vast amounts of agricultural production directly depend on the provisioning of such services (e.g. Klein et al., 2007, Costanza et al., 2014), we see a need to integrate ecosystem services into the land-sharing/-sparing discussion.

Land-sharing primarily favours those species that are adapted to agriculture or that use the agricultural matrix for foraging and reproduction (Phalan, Onial, et al., 2011). We contend that many of these species are instrumental for provisioning ecosystem services to agriculture. In particular, land-sharing is an effective strategy to promote pollination and biological pest control (Senapathi et al., 2015).

In contrast, land-sparing segregates biodiversity conservation from production, which can limit service provision from spared biodiversity to agriculture by disrupting species spillover, that is, cross-habitat fluxes of organisms coupling different habitats and enhancing ecosystem functioning in the habitat where the organism moves to (Blitzer et al., 2012; Tscharntke, Rand, & Bianchi, 2005). Nevertheless, land-sparing is the only way for in situ conservation of those species that require undisturbed natural habitats and are thus incompatible with agriculture within a land-sharing context.

Most species nowadays occur in fragmented habitats, either naturally or because of human alteration of landscapes (Fahrig, 2003). Their persistence depends on the formation of metapopulations (a set of local populations of a single species linked by dispersal; Gilpin & Hanski, 1991) and/or metacommunities (local communities linked by dispersal of multiple interacting species; Leibold et al., 2004; Wilson, 1992). To facilitate species dispersal and the persistence of spatially connected subpopulations, high connectivity between habitat patches is pivotal (Hastings & Botsford, 2006; White & Smith, 2018). Consequently, connectivity is also critical for the success of land-sharing and land-sparing measures: even large areas of spared land may fail to sustain viable populations in the long-term if immigration from the surrounding landscape is lacking (Halley, Monokrousos, Mazaris, Newmark, & Vokou, 2016). Sharing measures can create a more-biodiversity-friendly agricultural matrix that can increase the survival rates of crossing species. Moreover, areas under sharing measures can rescue service-providing species from connected areas with high fluctuations in temporal resource availability (Kremen, 2015; Mitchell, Bennett, & Gonzalez, 2013) and promote spillover of ecosystem services to intensively cultivated land (Blitzer et al., 2012).

Here, we follow previous calls to include both land-sharing and land-sparing measures to balance management needs for the multifunctionality of agricultural landscapes (Kremen, 2015; Tscharntke et al., 2012). We highlight the complementarity of both approaches by demonstrating that land-sharing is effective to promote ecosystem services in agricultural landscapes, while land-sparing is essential for the conservation of species that are incompatible with agricultural production. Moreover, we find that depending on the ecological and management context, the opposite is also frequently true. Land-sharing is crucial for the conservation of many nowadays endangered farmland species, and land-sparing ensures species communities with high response diversity (the range of reactions to environmental changes among those species contributing to the same ecosystem function or service; Elmqvist et al., 2003) that can stabilize the provisioning of ecosystem services in ever-changing landscapes. We conclude that both approaches need to be combined and integrated into a landscape connectivity matrix that optimizes the spatial linkages between natural habitats and production areas to facilitate movement of species. This is because high connectivity between land-sharing/-sparing measures and production areas is crucial to (a) promote the spillover of ecosystem services from land-sharing/-sparing measures to agricultural production and rescue service-providing species from hostile areas, (b) to facilitate immigration and counteract possible extinctions in spared habitats and (c) to conserve response diversity of species communities for ensuring resilience of ecosystem services in changing environments.

2 | LAND-SHARING FOR PROVISIONING ECOSYSTEM SERVICES

The land-sharing strategy focuses on landscapes dominated by agriculture, as agricultural production is linked to agrobiodiversity. Agrobiodiversity includes 'planned biodiversity' (e.g. the cultivated crop species or planted trees for shade management) and 'associated biodiversity' (e.g. species using crop resources or living in the agricultural matrix adjacent to production areas; Leakey, 2014; Tscharntke et al., 2011). Many species provide ecosystem services that are crucial for agricultural production and cannot be neglected in agricultural management (Cardinale et al., 2012; Myers, 1996; Zhang, Ricketts, Kremen, Carney, & Swinton, 2007).

Two of the most important services from associated biodiversity for agricultural production are crop pollination and biological pest control (e.g. Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005, 2012). Animal pollination increases yields of 75% of the world's economically most important global crops (Klein et

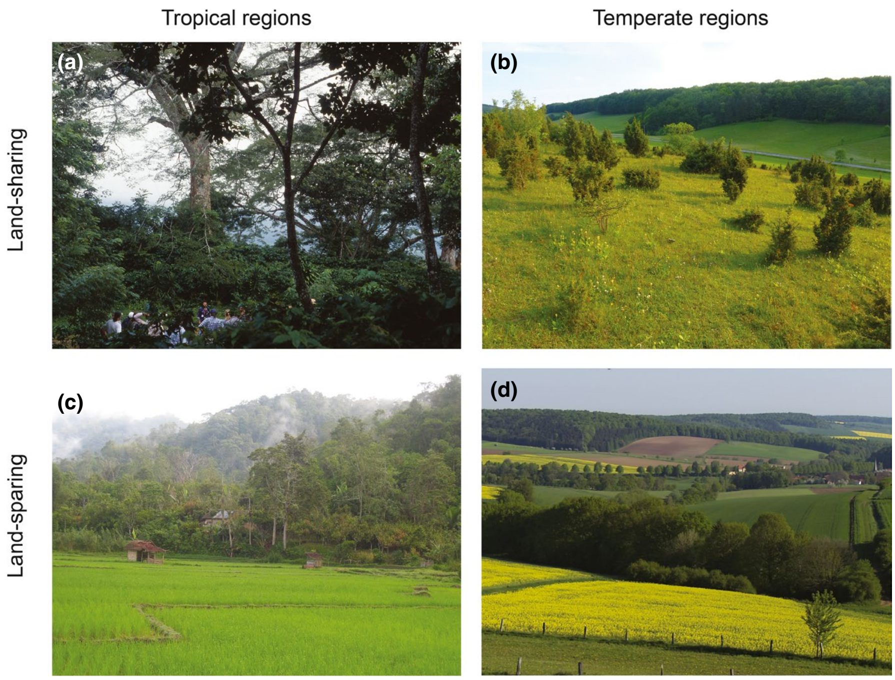

FIGURE 1 Examples of land-sharing and land-sparing in tropical and temperate regions: (a) coffee agroforestry in Nicaragua, (b) calcareous grassland in Germany, (c) rice agriculture next to forest reserve in Indonesia, and (d) forest fragment surrounded by intensively managed agricultural crops in Germany

al., 2007). Moreover, animal-pollinated crops contribute to diverse and healthy human diets as they contain essential micronutrients (Chaplin-Kramer et al., 2014; Eilers, Kremen, Greenleaf, Garber, & Klein, 2011). Despite the wide-spread use of managed pollinators, such as honeybees (*Apis mellifera*) (Aizen & Harder, 2009), pollination largely depends on wild pollinator species that rely on resources outside of production areas, such as wildflowers in the surrounding landscape matrix (Garibaldi et al., 2011, 2013; Kremen, Williams, & Thorp, 2002). Hence, land-sparing strategies that combine intensive agricultural production with the spatial segregation of habitats from crop-production areas can threaten local provisioning of ecosystem services to agriculture and thereby even reduce crop yields. (Chaplin-Kramer et al., 2014; Rusch et al., 2016; Tscharntke et al., 2012). In contrast, land-sharing approaches can conserve and restore functionally diverse pollinator communities, stabilizing pollination services within agricultural production areas (Hass et al., 2018).

Biological control of crop pests is a critical ecosystem service in industrial and small-scale farming. An estimated 30%–40% of global crop yields are lost to pest before harvest; crop losses are generally most severe in tropical regions where they can reach up to 100% (Oerke, 2006). The rise of chemical-intensive agriculture since the 1950s and the genetic engineering of insect-resistance crops since the 1990s has failed to significantly reduce crop losses due to pests (Oerke, 2006; Pimentel et al., 1992) but promoted pesticide resistance and dependencies of farmers on chemical and biotech companies (Jacobsen, Sørensen, Pedersen, & Weiner, 2013). Despite adverse effects on the environment, compromising natural biocontrol (Settle et al., 1996; Tscharntke et al., 2016) and human health, pesticide use is expected to triple by 2050 (Tilman et al., 2001). An alternative environmentally friendly strategy to prevent build-up of pest populations to economically damaging levels is to promote their natural enemies. Enhancing natural biological control in agricultural systems is of high economic, ecological and social interest (Bianchi, Booij, & Tscharntke, 2006; Naranjo, Ellsworth, & Frisvold, 2015; Oerke, 2006) and can be achieved through increasing spatio-temporal habitat heterogeneity within production systems (Sann et al., 2018).

A land-sharing approach in which biodiversity conservation is integrated into wildlife-friendly agricultural production optimizes the provisioning of pollination and biocontrol services to crop production (Pywell et al., 2015). Although not all pollinator or natural enemy species may be conserved, land-sharing landscapes can maintain high numbers of generalist species on which ecosystem services depend (Clough et al., 2011; Pywell et al., 2012; Senapathi et al., 2015). Land-sharing may be particularly efficient if the associated measures span multiple scales from small-scale infield solutions (e.g. intercropping or beetle banks) to large-scale structurally diverse agricultural matrices. Managing for pollinators or natural enemies is often easily achieved: for example, riparian buffers, weedy borders and beetle banks within fields can usually be implemented at little or no cost to farmers (Kremen & Chaplin-Kramer, 2007; Kremen & Miles, 2012). Hedgerows and non-cropped areas—often on marginal land of low productive value—provide habitat and resources for pollinators and natural enemies at times when resources from agricultural areas are limited (Kremen & Chaplin-Kramer, 2007). Implementing flower strips adjacent to production areas benefits biodiversity and enhances provisioning of ecosystem services to agriculture (Blaauw & Isaacs, 2014; Grass et al., 2016). For example, flower strips tailored to improving biological control in winter wheat can reduce crop damage by cereal leaf beetles by 40% and increase wheat yields at field borders up to 10% (Tschumi et al., 2016). These and other management actions at multiple spatial scales can be mixed to promote the desired services from associated biodiversity (Kremen, 2005). Importantly, even small increases in pollinator or natural enemy diversity can already benefit agricultural production. For example, 80% of the global pollination services to crops are carried out by only 2% of the species from regional species pools (Kleijn et al., 2015). These are typically common species, not of conservation concern, that thrive in a land-sharing context (Kleijn et al., 2015; Senapathi et al., 2015). Similarly, farmland can harbour high diversity of predatory species, but only few provide major contributions to biological control (Clough, Kruess, & Tscharntke, 2007; Flohre et al., 2011).

Land-sharing can also enhance the temporal stability of agricultural production. Yields of coffee and cocoa grown in shaded agroforestry systems are more stable over time than those of conventionally sun-grown crops that suffer from long-term 'boom and bust' cycles in which initial high yields are followed by unmanageable pest and pathogen outbreaks (Tscharntke et al., 2011). Similarly, successful biocontrol of crop pests needs both soil- and vegetation-dwelling enemies (Dainese, Schneider, Krauss, & Steffan-Dewenter, 2017; Rusch et al., 2016; Thies et al., 2011). Land-sharing practices are often prioritized when long-term sustainability is desired (Geertsema et al., 2016), in contrast to conventional intensification of agriculture that seeks short-term solutions to achieve highest crop production levels. For example, initial yield increases from conventional pesticides may come at the expense of newly emerging pests, adverse effects on non-target organisms and the evolution of pesticide resistance (Kremen, Iles, & Bacon, 2012; Palumbi, 2001).

Many traditional agricultural landscapes harbour rich biodiversity that has evolved over the past millennia but has faced unprecedented recent declines (Gaston, 2010). For example, European landscapes have been shaped by agriculture for centuries, resulting in strong feedback and interactions between farmland biodiversity and agricultural practices. However, agricultural intensification in the 20th century has resulted in widespread abandonment of traditional, extensive farming practices, followed by considerable biodiversity declines. Today, Europe's endangered farmland biota includes formerly widespread high-diversity groups such as arable non-crop plants and associated arthropods, non-fodder plants of dry grasslands, farmland birds, small mammals and charismatic species that are highly valued by the general public and conservationists, for example, hamsters, storks or hares (Herzog & Schüepp, 2013). The loss of biodiversity is particularly visible for farmland plants: of the 582 plant species adapted to arable habitats across 29 European countries, an average of 31% per country are nowadays considered rare or threatened (Storkey, Meyer, Still, & Leuschner, 2012).

A land-sparing perspective that only focuses on conserving non-farmed areas for biodiversity (e.g. unmanaged or natural land) is at odds with the fact that in landscapes with a long agricultural tradition, constant management and use of traditional agroecosystems are needed for conservation (Loos & von Wehrden, 2018; Poschlod & WallisDeVries, 2002). Conservation in most European countries focuses on these extensively managed systems, which can also provide ecosystem services to neighbouring fields such as pollination and biological control through spillover processes (Castle, Grass, & Westphal, 2019; Holzschuh, Dormann, Tscharntke, & Steffan-Dewenter, 2011; Holzschuh, Steffan-dewenter, & Tscharntke, 2009; Woodcock et al., 2016). Moreover, extensively managed systems such as calcareous grasslands can harbour some of the highest biodiversity levels per unit area, and also provide crucial refuges for plants and invertebrates of highest conservation concern (Kormann et al., 2015; Poschlod & WallisDeVries, 2002). However, their maintenance requires constant extensive usage (e.g. by mowing or grazing with livestock) to avoid succession of woody vegetation, which can only be realized in a land-sharing context.

3 | LAND-SPARING FOR BIODIVERSITY CONSERVATION

While land-sharing is needed to preserve farmland species and generalists, there are many species that cannot persist in intensively managed areas and simplified landscapes (Gámez-Virués et al., 2015). Agricultural expansion still commonly happens at the expense of natural ecosystems that support unique biodiversity. In many tropical landscapes, pristine habitats are threatened by expansion of agricultural land that supports only few generalist or non-native species of low conservation concern (Laurance, Sayer, & Cassman, 2014). It is therefore no surprise that a large body of the literature in favour of land-sparing for biodiversity conservation focuses on tropical landscapes (Edwards, Gilroy, Thomas, Uribe, & Haugaasen, 2015; Phalan, Onial, et al., 2011). Even if land-sharing conserves high species richness, species' populations often decline when compared to natural habitats (Phalan, Onial, et al., 2011). Studies that address biodiversity changes for a wide number of taxa at the population level are still few, but the number of 'losers' from adopting a land-sharing strategy can outweigh the number of 'winning' species, thus favouring a land-sparing strategy to reconcile biodiversity conservation with agricultural production (Phalan, Onial, et al., 2011). In general, primary habitats are irreplaceable for biodiversity (Gibson et al., 2011). Large and continuous habitat blocks that minimize negative effects of habitat fragmentation are usually most preferable, particularly for conservation of species that avoid habitat edges (Pfeifer, Lefebvre, Peres, & Etc, 2017) or that are associated with native habitats (e.g. insectivorous birds of the forest understorey; Maas et al., 2009).

There is no doubt that local, regional and international policies need to protect the pristine areas that still exist despite increasing pressure from human land use. Such undisturbed natural land supports high biodiversity and high levels of endangered species that need protection to mitigate current erosion of global biodiversity (Phalan, Onial, et al., 2011). Even the majority of predatory and pollinating species, which may be ecosystem service providers, depend on resources outside agricultural areas (Bianchi, Schellhorn, & Cunningham, 2013; Mandelik, Winfree, Neeson, & Kremen, 2012). However, many tropical protected areas fail to meet conservation targets because of weak law enforcement, illegal activities within their boundaries (e.g. logging) and a multitude of pressures from surrounding anthropogenic activities (Laurance et al., 2012). Economic globalization implies that agricultural intensification through land-sparing causes expansion of agricultural land, because protected land is merely replaced by imports from land use elsewhere (Lambin & Meyfroidt, 2011). Higher yield and profitability of intensified land use can attract migrants and consequently increase deforestation rates, contrary to the assumption that yield increases take pressure off protected land (Angelsen, 2010; Tscharntke et al., 2012). Good governance of protected areas and efficient management of productive land are therefore pivotal for land-sparing to be successful (Kremen, 2015; Lambin & Meyfroidt, 2011), which however, also needs careful consideration of the social and political context. In particular, land-sparing touches on the debate regarding conservation, human rights and poverty reduction. Excluding traditional inhabitants or land-users from protected areas may be ethically objectionable, can contribute to the destruction of cultural identity (e.g. nomadic herders) and might negatively impact the ecosystem in questions (e.g. through lack of management) (Naughton-Treves, Holland, & Brandon, 2005).

As discussed above, land-sharing can be an appropriate strategy for landscapes with a long tradition of extensive agriculture. However, landscapes that lack such tradition or historically separated conservation from agricultural areas might require a land-sparing strategy. The United States of America and Australia mainly rely on a land-sparing strategy in that their conservation measures focus on big National Parks and other protected areas, whereas agricultural land is predominantly devoted to production and yield maximization. In particular, invasive weeds play an important role in agriculture and (semi-)natural habitats can be a major source of pests. The non-native weeds in (semi-)natural habitats can host natural enemies, but they often host far more pests, whereas native plants mainly support natural enemies but rarely host pests of crops (Parry et al., 2015; Schellhorn, Glatz, & Wood, 2010; Tscharntke et al., 2016). In the Midwest United States, the dominant winter hosts of Asian soybean aphid *Aphis glycines* are European buckthorn *Rhamnus cathartica* and glossy buckthorn *Rhamnus frangula*, non-native shrubs that have invaded the woodlands of the Great Lakes states (Heimpel et al., 2010). Under these circumstances, farmers may remove remnants of (semi-)natural habitats adjacent to production areas and therefore will favour a land-sparing strategy (Tscharntke et al., 2016).

Land-sparing is also important to maintain response diversity of communities that sustains ecosystem functioning and services in future landscapes. Response diversity emerges from the diversity of different responses of species within a community to environmental change and is most important under heterogeneous conditions in space and time (Elmqvist et al., 2003; Tylianakis et al., 2008). In times of global change, current species performances may not predict those in future conditions; hence, response diversity, especially in large protected areas, may become critical for future ecosystem functioning. For example, climate change may lead to phenological mismatches among pollinators and crop flowering, necessitating a high response diversity in the thermal niches of crop pollinators (Fründ, Dormann, Holzschuh, & Tscharntke, 2013a; Kühsel & Blüthgen, 2015) and a diversity of responses to hibernation under increasing winter temperatures (Fründ, Zieger, & Tscharntke, 2013b). Likewise, spatial mismatches occur when the configuration of productive land does not overlap with the foraging ranges and habitat preferences or resources of pollinators (Ricketts et al., 2008) or natural enemies of crop pests (Tscharntke et al., 2016). Hence, apart from its contribution to biodiversity conservation, response diversity from land-sparing also enhances the resilience of ecosystem services in dynamic agricultural landscapes. This can be furthermore complemented by land-sharing measures, as suggested by the higher response diversity of ecosystem service-providing arthropods in diversified agriculture compared to conventional farming (Lichtenberg et al., 2017) and the conferring effects of high response diversity of bird communities on the resilience of their functions in low-intensity agricultural land in tropical countryside (Karp, Ziv, Zook, Ehrlich, & Daily, 2011).

4 | INTEGRATING LAND-SHARING AND LAND-SPARING STRATEGIES INTO A LANDSCAPE CONNECTIVITY MATRIX

Land-sharing and land-sparing measures cover wide ranges of management intensity, biodiversity value and spatial scale (Figure 2a). For all measures to be effective, they need to be strongly integrated into the agricultural landscape (Kremen, 2015; Mitchell et al., 2013). Thereby, high connectivity of the matrix is required to facilitate frequent dispersal and (re)colonization of habitat patches by species (Gilpin & Hanski, 1991; Leibold et al., 2004; Perfecto & Vandermeer, 2010) (Figure 2b). In today's human-modified landscapes, species need to be able to track changes in environmental conditions to avoid deterministic extinctions (e.g. because of habitat loss) and to colonize novel suitable patches (Thomas, 1994). In tropical land-sparing landscapes, this can be achieved by countryside elements, such as small forest patches on steep terrain, buffer vegetation along property boundaries or rivers and single trees (Hass et al., 2018; Kormann et al., 2016; Medina, Harvey, Sánchez Merlo, Vílchez, & Hernández, 2007; Mendenhall, Shields-Estrada, Krishnaswami, & Daily, 2016). Likewise, live fences of planted trees provide important habitat and resources for wildlife in Central American cattle rangelands and improve connectivity across these often intensively managed landscapes (Harvey et al., 2005). Stepping stones and corridors for species dispersal furthermore connect agricultural land to large blocks of spared natural habitat (Batáry et al., 2017; Holzschuh et al., 2009; Kormann et al., 2016; Medina et al., 2007; Şekercioğlu et al., 2015). Thereby, increased landscape connectivity also enhances the provision of ecosystem services such as pollination or pest control (Castle et al., 2019; Kormann et al., 2016; Mitchell et al., 2013; Şekercioğlu et al., 2015).

In contrast to an integrated approach, neglecting land-sharing practices to solely focus on sparing land for species conservation will fail to stop the ongoing losses of biodiversity. Populations in isolated nature reserves that are embedded in a homogeneous agricultural matrix, hostile to many species (Gámez-Virués et al., 2015), are mainly exposed to extinction forces only (Perfecto & Vandermeer, 2010; Tscharntke & Brandl, 2004). Hence, species in blocks of spared natural habitat may suffer from extinction lags if influx of individuals or gene flow are limited (Habel & Schmitt, 2018; Manning, Fischer, & Lindenmayer, 2006). As a result, even the largest protected areas lose species over the long term if they are situated in landscapes with very poor connectivity (Halley et al., 2016). Vice versa, land-sharing without complementary land-sparing measures can be equally ineffective: in the Colombian Chocó-Andes, the persistence of bird and dung beetle communities in low-intensity pastoral agriculture strongly depends on connectivity to surrounding forests, necessitating both the promotion of wildlife-friendly habitats and the protection of natural habitats for biodiversity conservation (Gilroy, Edwards, Medina Uribe, Haugaasen, & Edwards, 2014). Similarly, Kremen and Merenlander (2018) highlight the value of silvopasture as a wildlife-friendly land-sharing approach to cattle production that increases landscape connectivity in former monoculture agricultural lands interspersed with forest fragments. These studies add to the increasing evidence in favour of combining both land-sharing and land-sparing approaches for successfully reconciling biodiversity conservation with agricultural production (Klein, Steffan-Dewenter, & Tscharntke, 2003; Kremen, 2015; Kremen & Merenlender, 2018).

A comprehensive landscape management strategy requires a structurally diverse agricultural matrix that connects spared and shared habitats, allowing for metacommunity dynamics (Mitchell et al., 2013; Vandermeer & Perfecto, 2007). In some landscapes that are already devoid of such a connectivity matrix, this can require re-designing landscapes towards greater complexity (Kremen & Merenlender, 2018; Landis, 2017). In South East Asia, increasing political and socioeconomic pressure for more biodiversity-friendly production of biofuels has led to calls for re-designing oil palm landscapes, including land-sharing and land-sparing measures embedded within a connectivity matrix to reconcile biodiversity conservation with agricultural production (Koh, Levang, & Ghazoul, 2009). Scientists need to become actively involved in these debates, in particular by framing the scientific evidence to the questions and decisions of policymakers (e.g. distilling scientific results for answering key questions of landscape design such as minimum habitat area requirements of viable populations; Lucey et al., 2016).

We envisage that land-sharing/-sparing landscapes with high spatial connectivity (Figure 2) allow combining biodiversity conservation with multifunctional ecosystems. From an ecological point of view, landscape design may be guided by studies on landscape-wide biodiversity monitoring, spillover of species and associated ecosystem services between habitats and landscape elements (Kormann et al., 2016; Scherber, Beduschi, & Tscharntke, 2018; Tschumi et al., 2016; Woodcock et al., 2016). On regional scales, graph theory provides an analytical framework for identifying areas of low and high landscape connectivity as well as those habitats or landscape elements that facilitate metacommunity dynamics and thus population persistence (Urban & Keitt, 2001). Novel approaches that include temporal dynamics in species movements to understand spatiotemporal variation in landscape connectivity and habitat use, allow for more accurate estimations of isolation and extinction probabilities of populations (Martensen, Saura, & Fortin, 2017).

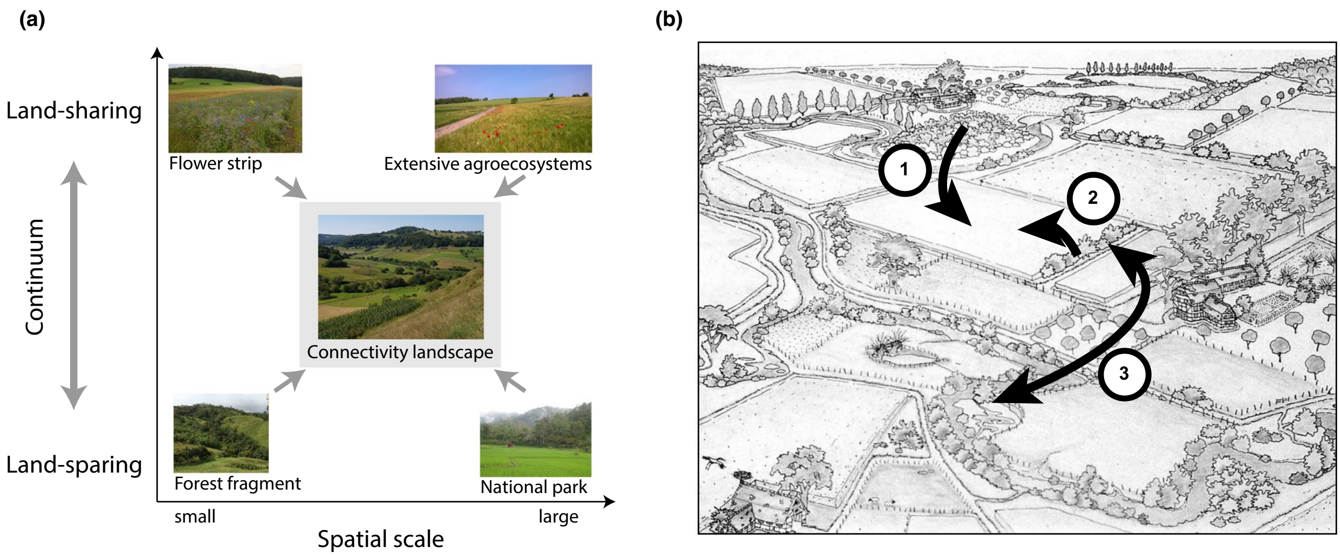

FIGURE 2 Land-sharing/-sparing connectivity landscapes. (a) Land-sharing and land-sparing measures cover multiple spatial scales and fall along a sharing–sparing continuum. Their combination in land-sharing/-sparing connectivity landscapes promotes both biodiversity conservation and the provisioning of ecosystem services. (b) High connectivity across the agricultural landscape matrix is needed for land-sharing and land-sparing to be successful. The connectivity matrix ensures (1) spillover from (spared) natural habitats to agroecosystems as well as (2) spillover from (shared) crop boundaries to agroecosystems. In addition, (3) landscape connectivity facilitates immigration and species dispersal, counteracting possible extinctions in spared habitats and providing response diversity in changing environments

For their successful implementation, considering the spatial scale of land-sharing/-sparing measures is crucial (Fischer et al., 2014). However, landscape design should not be hampered by the view that land-sparing always equals large blocks of habitats and land-sharing only refers to small-scale measures within agriculture. In fact, land-sparing and land-sharing measures vary strongly in their spatial extent and thus scale of implementation. Some authors argue that even smaller and less natural habitat patches can be considered land-sparing strategies when their creation requires taking land out of production (Ekroos et al., 2016). This may already be the case for small-scale measures that are typically not considered as land-sparing, such as the implementation of wildflower plantings on edges of crop fields. From this point of view, land-sharing would only apply to infield management (e.g. organic farming practices that conserve arable plants), whereas any land taken out of agricultural production for biodiversity conservation would be considered land-sparing (Batáry, Dicks, Kleijn, & Sutherland, 2015). Obviously, such matters of definition also depend on the target organism(s); likewise, small-scale measures for land-sparing only apply for species with very limited foraging ranges and strong habitat associations (Phalan, Balmford, Green, & Scharlemann, 2011). Often, there is no single correct spatial scale to segregate biodiversity conservation from agricultural production. Instead, targeted approaches for biodiversity, production and ecosystem services in multifunctional landscapes may require a 'multiple-scale land-sparing' (Ekroos et al., 2016; Lindgren, Lindborg, & Cousins, 2018). Furthermore, species that are sensitive to any human interference and in favour of large undisturbed natural remnants would completely disappear under a strategy focusing mainly on small natural patches in a hostile environment. This would compromise the original idea of land-sparing for the majority of rare and endangered species. In conclusion, there is a need to protect both small and large natural fragments across landscapes in an intermediate habitat fragmentation strategy to maximise conservation outcomes (Rösch, Tscharntke, Scherber, & Batáry, 2015; Wintle et al., 2019).

Finally, a diverse landscape that combines land-sharing and land-sparing within a heterogeneous connectivity matrix also strengthens other ecosystem services that are traditionally outside the main focus of landscape management. However, landscapes are multi-faceted and not restricted to simple production and biodiversity functions (Bennett, 2017; Geertsema et al., 2016). People are often emotionally linked to their home region and wish to experience cultural ecosystem services from the landscapes in their surroundings (Díaz et al., 2018; Plieninger, Dijks, Oteros-Rozas, & Bieling, 2013). Diversified landscapes have the potential to strengthen the bond between the local environment and its inhabitants.

5 | CONCLUSIONS

The land-sharing versus land-sparing debate has stimulated engaging discussions and innovative research. However, the debate has stagnated recently, and it has become obvious that the binary nature of the framework does not suffice to capture the real-world complexity of conservation and production in today's agricultural landscapes. Moreover, the integration of ecosystem services into the land-sharing/land-sparing discussion has been mostly neglected so far.

Here, we argue that land-sharing and land-sparing are not mutually exclusive. Land-sharing is an effective strategy to promote ecosystem services that are essential to agricultural production, such as pollination or biological pest control. Land-sparing is needed to conserve species incompatible with agriculture, such as endemic or rare taxa as well as natural ecosystems. The benefits of land-sharing/-sparing will be scale-dependent, and require the integration of small and large habitat patches into a diverse landscape matrix that increases spatial connectivity, thereby reducing the extinction probability of service-providing as well as rare species, and ensuring response diversity in dynamic landscapes.

Designing landscapes that encompass targeted, context-specific land-sharing/-sparing measures within a landscape connectivity matrix will provide habitat for biodiversity conservation and ecosystem services. The design of these landscapes needs to be an inclusive approach, involving scientists and stakeholders from policy and society. Taking the ecological- and also social- and political context-dependency into account makes for far more complicated situations than a simple 'either-or' approach. Notwithstanding, targeted and regionally specific solutions are the only way to address complex questions such as reconciling biodiversity conservation with agricultural production in future multifunctional landscapes.

CONFLICT OF INTEREST

Nothing to declare.

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AUTHORS' CONTRIBUTIONS

I.G. to T.T. conceived the study. I.G. wrote the first draft of the manuscript. All authors contributed to revisions and approved the final version of this paper.

DATA ACCESSIBILITY

No data were included in the study.

ORCID

Ingo Grass https://orcid.org/0000-0001-7788-1940
Péter Batáry https://orcid.org/0000-0002-1017-6996
Maraja Riechers https://orcid.org/0000-0003-3916-8102

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