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ABSTRACT

Agriculture and development transform forest ecosystems to human-modified landscapes. Decades of research in ecology have generated myriad concepts for the appropriate management of these landscapes. Yet, these concepts are often contradictory and apply at different spatial scales, making the design of biodiversity-friendly landscapes challenging. Here, we combine concepts with empirical support to design optimal landscape scenarios for forest-dwelling species. The supported concepts indicate that appropriately sized landscapes should contain ≥40% forest cover, although higher percentages are likely needed in the tropics. Forest cover should be configured with ~10% in a very large forest patch, and the remaining 30% in many evenly-dispersed smaller patches and semi-natural treed elements (e.g. vegetation corridors). Importantly, the patches should be embedded in a high-quality matrix. The proposed landscape scenarios represent an optimal compromise between delivery of goods and services to humans and preserving most forest wildlife, and can therefore guide forest preservation and restoration strategies.

INTRODUCTION

Forests are the dominant terrestrial ecosystem on Earth (Pan *et al.* 2013), but they are being rapidly converted to non-forest land uses such as agriculture, mining, energy generation, and other infrastructure (Curtis *et al.* 2018). Together, these result in the net annual loss of >12 million hectares of forests (Hansen *et al.* 2013), including forests in the last wilderness areas on Earth (Watson *et al.* 2016). Much of the remaining forest is distributed in millions of tiny patches (global mean size = 13-17 ha; Taubert *et al.* 2018). Thus, forest species are increasingly obligated to inhabit human-modified forest landscapes (HMFLs), in which forest is embedded in a matrix of anthropic land cover with varying capacity to sustain forest species (Harvey *et al.* 2006; Watling *et al.* 2011; Mendenhall *et al.* 2013; Galán-Acedo *et al.* 2019a; Hendershot *et al.* 2020). Designing and implementing effective conservation strategies have never been so urgent for the future of forest species – and our own future, too (Washington 2013). Our guidelines for design of HMFLs are therefore of interest, not only to ecologists, but to natural resource managers in general.

Forests hold the vast majority of the world's terrestrial species (Primack 2014). In fact, the highest species richness for many taxa occurs in tropical forests (Hillebrand 2004), which are undergoing the highest rate of deforestation worldwide (Hansen *et al.* 2013). Some taxa are almost entirely limited to forests (IUCN 2019). For instance, 94% of the world's nonhuman primate species are forest dwellers (Galán-Acedo *et al.* 2019c). Forest loss is therefore considered a major driver of global biodiversity decline (Fahrig 2003; Newbold *et al.* 2016; Betts *et al.* 2017). In fact, populations of forest-dwelling species are declining worldwide (Green *et al.* 2019), and about 30% of all threatened species in terrestrial ecosystems are forest species (IUCN 2019).

The impact of forest loss can vary depending on how specialized species are for forest habitats. Forest-interior specialists (i.e. those that use forest interior as the primary habitat) are usually more strongly and negatively impacted by forest loss than forest generalists (i.e. those that use resources from forest interior, forest edges, regenerating forest stands, and other treed covers in agricultural lands) (Pardini *et al.* 2010; Benchimol & Peres 2013; Newbold *et al.* 2014; Morante-Filho *et al.* 2018; Galán-Acedo *et al.* 2019b). In fact, forest generalist species can do well in HMFLs (Pardini *et al.* 2010; Carrara *et al.* 2015; Morante-Filho *et al.* 2018; Arce-Peña *et al.* 2019), in part because they have high vagility, and can therefore use resources from different land cover types (Harvey *et al.* 2006; Asensio *et al.* 2009; Mendenhall *et al.* 2016; Ferreira *et al.* 2018; Galán-Acedo *et al.* 2019a; Frishkoff *et al.* 2019). Thus, different management strategies should be implemented to simultaneously benefit as many species as possible in HMFLs.

Protected areas have long been recognized as essential for biodiversity conservation. The Global Forest Resources Assessment indicates that most countries are increasingly protecting their forests: 7.7% of global forests were protected in 1990 while 16.3% were protected in 2015 (Morales-Hidalgo *et al.* 2015). This should improve the fate of forest species (Hannah *et al*. 2020). However, forest species within reserves are also influenced by their surrounding landscape, because human-caused disturbances (e.g. forest loss, hunting, logging, soil erosion, fire, etc.) outside reserves can erode biodiversity inside them (Wittemyer *et al.* 2008; Laurance *et al.* 2012; Watson *et al.* 2014). Therefore, efforts to conserve protected areas should be complemented by the design of HMFLs that benefit forest species both inside and outside of protected areas. In most cases, effective designs should incorporate strategies for increasing forest cover (restoration) and improving the quality of the surrounding anthropogenic matrix (Aronson & Alexander 2013; Melo *et al.* 2013; Crouzeilles *et al.* 2016; Brancalion *et al.* 2019; Hendershot *et al.* 2020).

What does such a landscape look like? In other words, what kind of conservation and restoration strategies should be prioritized in HMFLs to be of greatest benefit for both forest-specialist and generalist species? Various strategies have been proposed, including: (i) preserving and restoring as much forest as possible (Fahrig 2003; Galán-Acedo *et al.* 2019b); (ii) embedding productive lands into forest ecosystems (land sharing; Perfecto & Vandermeer 2010); (iii) isolating forest from areas used by humans (land sparing; Phalan 2018); (iv) creating ecological corridors between forest patches

(Gilbert-Norton *et al.* 2010); (v) maintaining a small number of large forest patches (Diamond 1975); (vi) maintaining a large number of small forest patches (Simberloff & Abele 1982; Fahrig 2017, 2020); and (vii) improving the quality of the anthropogenic matrix by reducing agricultural intensification (Hendershot *et al.* 2020), pesticide use (Sánchez-Bayo & Wyckhuys 2019), and hunting (Deere *et al*. 2020), and implementing measures to mitigate wildlife road-kill (Rytwinski & Fahrig 2015; Alamgir *et al*. 2017).

Here, we review key concepts on species responses to local (e.g. forest patch geometry) and landscape (e.g. amount of forest cover, number of forest patches) variables (Box 1), to prioritize management strategies for conservation of forest species (Table 1). Combining multiple concepts with broad support, we design hypothetical 'optimal landscape' scenarios for conservation of both forest-specialist and generalist species, including those with important ecological roles (e.g. seed dispersers) and that provide key ecosystem services (e.g. pest control). In particular, we address the following questions: Why is it important to preserve forest cover? How much forest needs to be maintained? How should forest be arranged in the landscape? What role can vegetation corridors and other semi-natural treed elements play in biodiversity conservation? Why are regenerating forests so important for wildlife conservation? How can matrix quality contribute to preventing species losses? And how must human settlements and infrastructure be managed? We note that to be sustainable, landscapes must be adequate not only for forest species, but also for humans. Therefore, we conclude by discussing some important benefits for ecosystem services in idealized HMFLs.

WHY IS IT IMPORTANT TO PRESERVE FOREST COVER?

Maintaining and increasing forest amount in HMFLs is of paramount importance (Fig. 1a; Table 1). Forest loss generally has larger negative effects on species responses than changes in forest configuration, such as fragmentation per se (Fahrig 2003, 2017; Jackson & Fahrig 2016; Carrara *et al.* 2015; Arroyo-Rodríguez *et al*. 2016; Klingbeil & Willig 2016; Arce-Peña *et al.* 2019; Galán-Acedo *et al.* 2019b; Watling *et al.* 2020). Available studies on the land sharing/sparing model also confirm the importance of protecting and restoring as much forest cover as possible (Phalan 2018, Table 1). In fact, landscape forest cover is positively related to forest resource availability (reviewed in Fahrig 2013), which increases population size, genetic diversity, and persistence of forest species (Fahrig 2003; Boscolo & Metzger 2011; Jackson & Fahrig 2016; Newbold *et al.* 2016; Betts *et al.* 2017).

Forest cover also brings important benefits for biological communities. It is consistently and positively related to species diversity of different taxa (Fahrig 2003; Carrara *et al.* 2015; Arroyo-Rodríguez et al. 2016; Newbold *et al.* 2016; Betts *et al.* 2017; Galán-Acedo *et al.* 2019b; Watling *et al.* 2020). This occurs directly through resource provisioning, and indirectly through positive species interactions. For instance, relaxation of competitive exclusion can favor species coexistence in more forested landscapes (Buchmann *et al.* 2013). Also, forest in high forest cover landscapes has complex vegetation structure and high fruit availability, positively affecting the diversity of tropical forest birds (Morante-Filho *et al.* 2018). Forest cover is also positively related to seed dispersal (Jesus *et al.* 2012; San-José *et al.* 2019), favoring forest recovery in HMFLs (Arroyo-Rodríguez *et al.* 2017b). Forest preservation can be particularly important in the tropics, where up to 90% of plant species are dispersed by forest animals, especially birds (Fleming *et al.* 1987; Markl *et al*. 2012), which can be negatively impacted by forest loss (Morante-Filho *et al.* 2015, 2018; Watling *et al.*

2020). Therefore, increasing forest cover in HMFLs is of paramount importance, not only for forest species, but for the ecological processes in which they are involved (Benchimol & Peres 2013; Carrara *et al.* 2015; Morante-Filho *et al.* 2018; Phalan 2018; Arce-Peña *et al.* 2019; Galán-Acedo *et al.* 2019b).

Forest cover influences biodiversity responses at both local and landscape scales (Table 1). At a local scale, forest embedded in largely deforested landscapes can be highly degraded, exhibiting greater canopy openness and lower tree basal area than in contiguous forest (Rocha-Santos *et al.* 2016). However, species richness in plots of fixed size (species density) are more strongly and positively related to landscape forest cover than to the geometry of the patch in which the plot is located (see the 'habitat amount hypothesis'; Fahrig 2013; Table 1). A recent global meta-analysis supports this prediction for mammals, amphibians, reptiles, birds, insects and plants (Watling *et al.* 2020). Therefore, conservation strategies should be designed and implemented at a landscape scale (not at a patch scale), considering forest cover as a top priority, especially in the wet tropics (Fig. 1a).

HOW MUCH FOREST NEEDS TO BE MAINTAINED IN A LANDSCAPE?

To answer this question we first need to consider the size or spatial extent of the landscape itself. We begin by identifying the forest species that we wish to maintain in the landscape. These could be species with low natural population density and/or of particular conservation value. We can then use population viability analyses to estimate the minimum total forest area needed for persistence of those species. Consider that most species require between 10–30% of habitat (here, forest) in the landscape to occur there (Andrén 1994; Swift & Hannon 2010). Therefore, a baseline estimate is that the landscape should be large enough that the minimum amount of forest needed for persistence of the focal species represents 30% of the landscape area. A recent study modeling 289,219 species indicates that preserving 30% of terrestrial ecosystems can reduce extinction risk by more than 50% (Hannah *et al*. 2020). Yet, extinction risk decreases with increasing area conserved (Hannah *et al*. 2020). Furthermore, density estimates and population viability analyses are inherently uncertain (Pe'er *et al.* 2014). Therefore, our conservative guideline is to maintain at least 40% of the appropriately sized landscape as forest to confidently ensure persistence of most forest species (Fig. 1b; Table 1). For example, if a species requires a few thousand square kilometers of forest to persist, as is usually the case for many large-bodied mammals and apex predators (Pe'er *et al.* 2014), an appropriate landscape size for these species will be tens of thousands of square kilometers. Yet, as most species have minimum habitat requirements of <1000 km^2 (Pe'er *et al.* 2014), smaller landscapes (e.g. <3000 km^2) may be adequate in many regions.

Where such large-scale planning is not possible (e.g. due to political boundaries), a network of smaller optimal landscapes could be implemented. This would be done with the understanding that a single smaller landscape would not contain sufficient forest for all species, but that a set of such landscapes in proximity could maximize conservation outcomes. Note that although our main focus is on conservation of forest species, a landscape with 40% forest should also maintain habitat generalist species, i.e. those that can persist both in forest and open habitats, as well as species that occur primarily in the matrix.

Our recommendation that forested landscapes include at least 40% cover echoes calls to preserve half of the Earth's natural area (Locke 2015; Wilson 2016; Dinerstein *et al.* 2017). This is actually a key target of the Convention on Biological Diversity's framework for 2050 (CBD Secretariat 2020). Such a degree of protection has been achieved in several regions (Hannah *et al*. 2020), and has proven to be highly successful for biodiversity conservation (see case studies in https://natureneedshalf.org/). In particular, it allows for the protection of very large amounts of forest in some areas, sufficient to maintain species that cannot persist in human-dominated landscapes. However, to successfully preserve most forest species, the 50% global conservation rule must be applied on a per-forest-type basis, i.e. we need to preserve 50% of each forest type in each ecoregion (Ellis 2019). In many areas, this would require massive restoration efforts to replace the forest that has already been lost, e.g. Brazilian Atlantic forest (Ribeiro *et al.* 2009; Melo *et al.* 2013). This is a challenging but achievable task (Fischer *et al.* 2008; Navarro & Pereira 2012; Phalan 2018; Brancalion *et al.* 2019).

The effectiveness of forest thresholds may depend on other variables, such as matrix quality (Table 1; Fig. 1b). In particular, there is a predicted interaction between the minimum habitat required for species persistence and matrix quality, such that more habitat is needed when the matrix is of lower quality (Fahrig 2001; Swift & Hannon 2010). We should therefore preserve more forest where the matrix is dominated by intensive agriculture (Boesing *et al.* 2018). This is because such land uses limit animal movement and reduce resource availability for forest-dwelling species (e.g. Watling *et al.* 2011; Galán-Acedo *et al.* 2019a), thus increasing their sensitivity to forest loss (Gascon *et al.* 1999; Fahrig 2001; Swift & Hannon 2010).

The minimum amount of forest should also be greater in tropical than in temperate regions (Fig. 1b; Table 1). This is because minimum habitat requirements appear to be higher for species with lower reproductive rates (Vance *et al*. 2003; Holland *et al.* 2005), small geographic ranges, and/or small population sizes (Swift & Hannon 2010). These traits appear to apply more generally to species near the equator

(Purvis *et al.* 2000). In fact, land-sparing strategies seem to be particularly valuable for species with smaller geographic ranges (Phalan 2018). Also, the impact of forest loss is generally stronger in more equatorial regions (Betts *et al.* 2019). These tropical-temperate differences may explain why recent studies in tropical forest landscapes found higher forest cover thresholds (25–50%) for plants, birds and insects (Rigueira *et al.* 2013; Morante-Filho *et al.* 2015; Boesing *et al.* 2018; Pinto *et al.* 2018) than those suggested by Andrén (1994). In fact, Lovejoy & Nobre (2018) suggest that 75-80% forest cover should be preserved in the Amazon to avoid major alterations of its hydrological cycle, and myriad cascading effects on biodiversity and human well-being in Brazil and adjacent South America (Walker *et al.* 2019). In response, the Brazilian Forest Code (now called 'Native Vegetation Protection Law') establishes that rural properties in the Amazon should preserve 80% of their native vegetation, though this target has been met with resistance (Azevedo *et al.* 2018).

HOW SHOULD FOREST BE ARRANGED IN A LANDSCAPE?

Landscape-scale assessments of different response variables (e.g. patch occupancy, population size, species diversity, diversity of threatened species) consistently indicate that for a given amount of forest, increasing the number/density of forest patches or forest edge density in the landscape (i.e. fragmentation per se) generally has weak effects on biodiversity (Fahrig 2003, 2017; Table 1). At the patch scale, some species show negative responses to forest edges (Fletcher *et al.* 2018). Yet, available studies that control for forest loss indicate that there must be mechanisms at a landscape scale (e.g. increased habitat diversity) that can counteract negative local edge effects (Fahrig 2017; Fahrig *et al.* 2019). Therefore, forest spatial configuration is not as important as forest cover (Fig. 1a). Most configurations should protect most forest species if enough forest is available in the landscape.

However, several lines of evidence indicate that maintaining a large number of small forest patches is generally more valuable for biodiversity conservation than maintaining a smaller number of large forest patches (Fig. 1c; Table 1). First, when significant, most responses to fragmentation per se are positive (Fahrig 2017; Table 1). Second, evidence from empirical SLOSS (Single Large or Several Small) studies shows that for a given amount of habitat, more small patches protect more species than fewer large patches (Simberloff & Abele 1982; Quinn & Harrison 1988; Fahrig 2020). Therefore, we suggest that distributing most (e.g. ~75%) of the remaining forest (i.e. 30% of the landscape) in many small forest patches will preserve more forest species in the landscape (Table 1). Many small patches are more likely than a few large patches to cover the full range of environmental heterogeneity (e.g. different soil types) in the landscape – an important management strategy for land sparing to succeed (Phalan 2018). Covering the entire environmental gradient increases the compositional dissimilarity of patch communities (i.e. β-diversity), accumulating a higher total (γ) diversity in the landscape (Karp *et al.* 2012; Arroyo-Rodríguez *et al.* 2013; Liu & Slik 2014; Fahrig 2020). This is particularly valuable in the tropics, where species turnover among localities is very high (Arroyo-Rodríguez *et al.* 2013; Solar *et al.* 2015).

There is increasing awareness of the very high conservation value of sets of small forest patches for global biodiversity (Arroyo-Rodríguez *et al.* 2009; Hernández-Ruedas *et al.* 2014; Fahrig *et al.* 2019; Palmeirim *et al.* 2019; Volenec & Dobson 2020; Wintle *et al.* 2019). Small patches can be included as part of a land-sparing strategy (Grass *et al.* 2019); for example, many insects and birds can maintain viable populations in patches of a few hectares (Pe'er *et al.* 2014). Small patches can preserve a large number of tropical trees and mammals, including endangered ones (Arroyo-Rodríguez *et al.* 2009; Garmendia *et al.* 2013; Hernández-Ruedas *et al.* 2014). Increasing the number of small patches in a given landscape reduces patch isolation (Fig. 1c), improving landscape connectivity and resource availability for forest species (Dunning *et al.* 1992; Uezu *et al.* 2008; Asensio *et al.* 2009). In fact, many ecological processes can be improved in landscapes with a large number of small forest patches (reviewed by Fahrig *et al.* 2019). For example, metapopulation persistence can increase with an increasing number of forest patches (Table 1). The reduction in inter-patch distance in fragmented landscapes can facilitate landscape supplementation (reviewed by Fahrig *et al.* 2019). Fragmentation per se can also favor species coexistence by preventing the proliferation of strong competitor species which can jeopardize biodiversity conservation in HMFLs (Hernández-Ruedas *et al.* 2018).

We cannot overlook that some forest species are negatively affected by fragmentation per se (Fahrig 2017). In fact, there are a few examples of species groups that do better in single large than in several small patches (Fahrig 2020). Some authors infer that forest interior species in the tropics may require large blocks of natural forest cover (Fletcher *et al.* 2018; Phalan 2018). We therefore suggest it is appropriate to retain ~25% of forest (~10% of the landscape) as a contiguous protected area in the landscape (Table 1; Fig. 1c). As described above, to preserve the few species that do better in large, contiguous patches, a landscape should be big enough so that 10% of it, exclusive of edges (e.g. 100-m wide edges; Laurance *et al.* 2002; Harper *et al.* 2005), exceeds the minimum area requirements for those species.

WHAT ROLE CAN VEGETATION CORRIDORS AND OTHER SEMI-NATURAL ELEMENTS PLAY IN BIODIVERSITY CONSERVATION?

Vegetation corridors include riparian forest strips and other semi-natural treed elements (e.g. hedges, windbreaks, living fences) that can be particularly valuable for conservation (Table 1). Riparian forest strips are critical for preserving forest species that depend on water bodies for reproduction, such as many insects, amphibians, and fish (Mitchell *et al.* 2018; Paoletti *et al.* 2018). Water is also a key resource for many forest reptiles, mammals and birds, for drinking, feeding, and resting (Hawes *et al.* 2008; Ribeiro *et al.* 2012; Zimbres *et al.* 2017). Riparian forest can also function as ecological corridors, improving ecological connectivity (sensu Fischer & Lindenmayer 2007). Therefore, the preservation and restoration of riparian forest should be prioritized (Fig. 1c).

Semi-natural treed elements in the matrix, such as hedges, windbreaks, living fences and even isolated native trees can also function as corridors or stepping stones (Table 1; Fig. 2) that can increase biodiversity in many landscapes (Tews *et al.* 2004; Harvey *et al.* 2005, 2006; Pulido-Santacruz & Renjifo 2009; Cadavid-Florez *et al.* 2019). In fact, these features are thought to be disproportionately valuable for increasing connectivity relative to the small proportion of landscape cover they represent (Beier & Noss 1998; Harvey *et al.* 2005, 2006; Uezu *et al.* 2008; Cushman *et al.* 2014; Kormann *et al.* 2016). They can also offer important resources for forest species, including cool microclimates, reproductive resources (e.g. nesting areas) and food (Harvey *et al.* 2005; Asensio *et al.* 2009; Pulido-Santacruz & Renjifo 2009; Galán-Acedo *et al.* 2019a). Because these resources are limited in the matrix, the value of isolated trees for wildlife may be greater – on a per-tree basis – than that of trees in a forest (Fischer *et al.* 2010; Robinson *et al.* 2013). For example, Asensio *et al.* (2009) showed that howler monkeys in highly deforested landscapes can use living fences and isolated trees to disperse and forage across the landscape, particularly when food resources in their home patches were very low. Therefore, the conservation value of these landscape elements will be higher if composed of native fruiting trees. Other studies demonstrate that corridors and isolated remnant trees can enhance landscape connectedness, pollination, seed dispersal and vegetation regeneration in HMFLs (e.g. Guevara & Lavorde 1993; Kormann *et al.* 2016; Cadavid-Florez *et al.* 2019). Scattered remnant trees can also act as discrete habitat patches for some small, forest species (e.g. Robinson *et al.* 2013). Therefore, these semi-natural elements play a key role in preserving biodiversity patterns and processes, and should be enhanced in HMFLs (Table 1; Fig. 1d; Fig. 2).

How much area should such small, semi-natural elements occupy in a landscape? In tropical regions where several of the benefits cited above have been documented, they occupy less than 4% of landscape area (e.g. Harvey *et al.* 2005; Asensio *et al.* 2009; Galán-Acedo *et al.* 2018; Cadavid-Florez *et al.* 2019). Thus, a small land area removed from production represents a large biodiversity benefit. Because they reduce the total amount of land left for human uses, we suggest that they be included as part of the 40% 'forest’ cover in an idealized landscape. On the other hand, where these elements have a relatively low opportunity cost, their coverage could be increased (Phalan 2018). For example, farmers in four tropical regions from Costa Rica and Nicaragua are aware that in addition to providing shade and wind protection, living fences in pastures can be important for cattle, “reducing heat stress, particularly in the dry season, and providing a more comfortable environment for cattle, resulting in higher weight gain, milk production and reproductive rates” (Harvey *et al.* 2005). In such cases, they can be considered as part of the production area of the landscape.

WHY ARE REGENERATING FOREST STANDS SO IMPORTANT FOR WILDLIFE CONSERVATION?

Recent estimates suggest that the cover of regenerating forest stands is increasing worldwide (Hansen *et al.* 2013). Forest regeneration on abandoned lands, especially long-abandoned areas, can increase tree biomass and species diversity (Poorter *et al.* 2016; Arroyo-Rodríguez *et al.* 2017b; Rozendaal *et al.* 2019). For example, aboveground biomass stocks in second-growth tropical forests take a median time of 66 years to recover to 90% of old-growth values (Poorter *et al.* 2016), and only five decades to recover the species richness of old-growth forest (Rozendaal *et al.* 2019). Thus, late successional second-growth forests are suitable habitat for many forest specialist species and can be classified as "forest" in the landscape (Chazdon *et al.* 2016).

But what about early (e.g. <50-yrs) successional forests? These forests are typically dominated by fast-growing, disturbance-adapted pioneer species (reviewed by Arroyo-Rodríguez *et al.* 2017b). In fact, tree species composition significantly differs between early successional tropical forests and old-growth forests (Rozendaal *et al.* 2019). Thus, young (and shrubby) forest types may only be used by a subset of forest species, and should only be considered as part of the 40% forest cover if old-growth forest is scarce or absent in the landscape.

The exclusion of early successional forests from estimates of forest cover is a conservative measure, as they cannot be considered substitutes for old-growth forests. Yet, they are still important for forest wildlife. For example, the multiple successional pathways that regenerating stands can follow implies that they can have different biotic and abiotic characteristics, contributing to increased heterogeneity, species turnover (β-diversity), and γ-diversity in the landscape (Arroyo-Rodríguez *et al.* 2017b). The maintenance of β-diversity in the landscape is critical because it can override the negative effects of land cover change on local (α) diversity (see the 'dominance of beta-diversity hypothesis' and empirical evidence in Tscharntke *et al.* 2012). Early successional forests can also enhance matrix permeability and landscape connectedness for old-growth forest species by operating as stepping stones and vegetation corridors (Harvey *et al.* 2008; Chazdon *et al.* 2009; Melo *et al.* 2013; Arroyo-Rodríguez *et al.* 2017b; Galán-Acedo *et al.* 2019a), and can help decrease negative edge effects (e.g. Mesquita *et al.* 1999). Therefore, they should be integrated into conservation-planning approaches in HMFLs (Harvey *et al.* 2008; Chazdon *et al.* 2009; Lindenmayer *et al.* 2008; Melo *et al.* 2013; Arroyo-Rodríguez *et al.* 2017b; Fig. 1d panel 1).

HOW CAN MATRIX QUALITY PREVENT SPECIES LOSSES?

Along with preserving forest, semi-natural elements and regenerating forest stands, improving matrix quality (i.e. the non-forest land covers in the landscape; Box 1) should be a top priority for designing biodiversity-friendly landscapes (Fig. 1d; Table 1). In fact, an increasing number of studies demonstrate that matrix quality is more important than forest spatial configuration for various taxa (turtles and birds: Quesnelle *et al.* 2013; bats: Arroyo-Rodríguez *et al.* 2016; dung beetles: Sánchez-de-Jesús *et al.* 2016; primates: Galán-Acedo *et al.* 2019b). Matrix quality is critical for buffering (or even eliminating) negative edge effects (Mesquita *et al.* 1999; Arroyo-Rodríguez *et al.* 2017a; Boesing *et al.* 2018), and for improving landscape connectivity (Uezu *et al.* 2008; Grass *et al.* 2019). The matrix is so important that forest-dwelling species that are able to use the matrix (including birds, frogs, small mammals and ants) can have a lower probability of extinction from forest loss than species that are unable to use the matrix (Gascon *et al.* 1999; Fahrig 2001; Swift & Hannon 2010; Boesing *et al.* 2018; Reider *et al.* 2018; Galán-Acedo *et al.* 2019a). A recent global and multi-taxa meta-analysis shows that species-area relationships are steeper in landscapes with low matrix quality, and shallower (less extinction driven) where matrix quality is higher (Reider *et al.* 2018). Another study found that forest primates that have been reported to use the matrix (e.g. human settlements, open areas, arboreal crops and/or clear cuts) are less threatened with extinction than matrix-avoiding species (Galán-Acedo *et al.* 2019a). Species that make use of the matrix thus require less forest in the landscape to survive, driving the interaction between habitat amount and matrix quality (Fahrig 2001). However, species that persist in the matrix often come from distinct clades, representing only a subset of the community tree of life (Frishkoff *et al.* 2014; Nowakowski *et al.* 2018c).

How can we increase matrix quality to promote its use by forest wildlife while minimizing its negative environmental impacts? Different practices have been proposed. First, treeless matrices (e.g. pastures, annual crops, roads, human settlements) should be avoided as much as possible, because they provide few resources for forest species and increase forest-matrix contrast, causing significant biotic and abiotic changes along forest edges (Laurance *et al.* 2002; Harper *et al.* 2005; Pfeifer *et al.* 2017; Fletcher *et al.* 2018; Hendershot *et al.* 2020). Yet, different agroecological practices can be adapted to improve the quality of these matrices. For example, the 'low-input agriculture' approach emphasizes adapting agricultural system to the environmental conditions of a region (e.g. soil, water, climate and biota), and optimizing the use of natural (biological and chemical/physical) resources present in the agroecosystem (reviewed by Pimentel *et al.* 1987). Reducing the use of pesticides (Sánchez-Bayos & Wyckhuys 2019), and enhancing biological pest control (Perfecto & Vandermeer 2010; Karp *et al.* 2013; Wanger *et al.* 2014; Grass *et al.* 2019) are particularly critical. This can be done by maintaining and planting native trees on farmlands to attract native species and the ecosystem services they provide (see below). Such combinations of native trees and crops on the same land are called 'agroforestry systems'. These include agrosilvicultural systems (a combination of annual crops and trees, including native trees and tree plantations, such as shaded cacao, coffee and yerba mate plantations), silvopastoral systems (which combine native/planted trees and grazing of domesticated animals on pastures or on-farm), and agrosilvopastoral systems (a combination of native/planted trees, animals and annual crops) (FAO 2019). These wildlife-friendly systems can provide relatively high yields, contributing to a land sparing strategy via 'sustainable intensification', 'ecological intensification' and 'agroecological intensification' practices (reviewed by Phalan 2018). In other words, high-yield farming does not necessarily imply the use of biodiversity-harmful agricultural practices, such as pesticides (Green *et al.* 2005; Phalan 2018). Some agroecological methods and agroforestry systems can increase yields at a relatively low environmental cost (Perfecto & Vandermeer 2008, 2010), and can therefore be enhanced to free up more land for forest conservation and restoration in HMFLs (Fig. 1d).

The benefits of agroforestry systems for forest wildlife are well documented. These productive systems can provide supplementary food resources, refuge and dispersal opportunities (Perfecto & Vandermeer 2008; Mendenhall *et al.* 2016; Ferreira *et al.* 2018; Galán-Acedo *et al.* 2019a; Grass *et al.* 2019; Frishkoff *et al.* 2019). However, agroforestry systems alone are unable to maintain most forest species, which usually depend on the preservation of landscape forest cover (Schroth *et al.* 2015).

Agroforestry systems are a valuable way to improve matrix quality in HMFLs, and should complement the preservation of old-growth forest, not replace it.

HOW MUST HUMAN SETTLEMENTS AND INFRASTRUCTURE BE MANAGED?

Roads typically cover little of a landscape, but their negative impact on biodiversity is well documented. Roads can increase mortality rates of forest species and limit interpatch movements (Rytwinski & Fahrig 2015; Bennett 2017). In their review, Muñoz *et al.* (2015) found that abundance and diversity of insects is negatively associated with roads because of high road mortality, and the unwillingness of many species to approach or cross roads in the first place. Amphibians and reptiles are also particularly susceptible to road mortality and habitat isolation by roads (Bennett 2017). The negative effects on species abundances can extend far beyond the physical footprint of the road into adjacent areas, resulting in so-called road-effects zones (Torres *et al.* 2016). In general, species vulnerability to roads depends on conservation status, geographical location, habitat preferences, road type, and traffic volume (Rytwinski & Fahrig 2015). Fences mitigate wildlife road-kill, and are legal obligations in some countries. In fact, a recent meta-analysis shows that exclusion fencing reduces road-kill by 40% compared to controls (Rytwinski *et al.* 2016). Such mitigation measures should be enhanced where possible. Polak *et al.* (2019) found that planning for the needs of all species in the landscape maximizes the number of persisting species and is more cost-effective than focusing on single species. Thus, it is critical to include multi-species strategies for mitigating road-kills in biodiversity-friendly landscapes.

Small rural communities and villages are common in HMFLs. The people living in these settlements can directly impact biodiversity through the exploitation of forest resources, and indirectly through forest disturbance (Melo *et al.* 2013). Examples include hunting, extraction of firewood and non-timber forest products, and the damage caused by livestock. These processes result in a subtle but constant loss of diversity and forest biomass, even in landscapes with high forest cover (Laurance & Peres 2006; Melo *et al.* 2013; Barlow *et al.* 2016; Benítez-López *et al.* 2019; Osuri *et al.* 2020). Such threats are often magnified by road construction (Laurance *et al.* 2009). In fact, many negative effects attributed to fragmentation are likely the result of human activities in the matrix, rather than a response to forest configuration itself. For instance, hunting strongly increases species vulnerability to anthropogenic disturbances (Lamb *et al.* 2017; Benítez-López *et al.* 2019; Osuri *et al.* 2020). Large-bodied vertebrates are a good example. They have been severely hunted, especially in tropical forests, resulting in "empty" or "half-empty" forests (Peres & Palacios 2007). This defaunation process affects ecosystem processes such as seed dispersal and carbon cycling (Bello et al 2015; Peres *et al.* 2016). Educational programs with the people living in the vicinity of forest is therefore key to maintain forest species in the landscape (Chapron *et al.* 2014; Asensio *et al.* 2009; May 2010; Galán-Acedo *et al.* 2019a).

Enforcement of environmental regulations is also important to minimize defaunation by illegal hunting and trade of native forest species. There is a large body of literature describing the impact of these practices on natural ecosystems (Lamb *et al.* 2017; Benítez-López *et al.* 2019; Osuri *et al.* 2020). Effective field-based enforcement requires structured governance, significant financial resources and low corruption – conditions that are largely lacking in some developing countries (Börner *et al.* 2014). Yet, care should be taken with command-and-control approaches in HMFLs characterized by traditional (indigenous or not) people that hunt for subsistence and share wild meat to establish social relationships (Nunes *et al.* 2019a). The prohibition of subsistence hunting in such landscapes may induce more deforestation for protein production and be unrealistic for monetarily deprived forest dwellers (Nunes *et al.* 2019b). Achieving an optimal landscape scenario requires understanding the socioecological characteristics of the area.

HUMAN BENEFITS IN BIODIVERSITY-FRIENDLY LANDSCAPES

The biodiversity-friendly landscape scenarios proposed here maximize conservation benefit, yet can also improve human well-being by helping to maintain essential goods and ecosystem services for people. In fact, as argued by Melo et al. (2013), moderately-managed landscapes such as those proposed here optimize the delivery of goods and services (Fig. 3). Among other goods, the remaining forest and treed elements in the matrix can provide timber, pulpwood, firewood, fodder, non-conventional food plants, meat, cash crops, fish and medicinal plants for local communities (Balvanera *et al.* 2006; Diaz *et al.* 2006; Harvey *et al.* 2006; FAO 2019). Remnant forest also provides four key types of services: the regulation of climatic conditions, maintenance of water quantity and quality, crop pollination, and biological pest control (Balvanera *et al.* 2006; Diaz *et al.* 2006; Kormann *et al.* 2016; Lovejoy & Nobre 2018; Grass *et al.* 2019).

Regulation of climatic conditions

Forests play a crucial role in climate regulation. Tropical forests, for example, are critical carbon sinks with total storage up to 861.7 ± 80.2 Tg C year^{-1} (Baccini *et al.*

2017). Large trees (>30 cm diameter) are the principal components of aboveground biomass in tropical forests (Fauset *et al.* 2015), and hence, increasing forest cover and treed elements in the matrix can help increase carbon storage, potentially buffering ongoing climate change (Houghton 2005). Regenerating stands and agroforestry systems are also important in the context of climate change adaptation (Schroth *et al.* 2015; Poorter *et al.* 2016). In the Brazilian Atlantic forest, for example, regenerating forests can recover ~20% of the aboveground carbon stocks of a primary forest in only three decades after land abandonment (Matos *et al.* 2019). Carbon storage in some cocoa agroforestry systems can be ~60% of that of natural forests, suggesting that "1.6 ha of optimally managed agroforest could contribute to the conservation of carbon stocks as much as 1 ha of natural forest" (Kessler *et al.* 2012).

Forest cover and fragmentation per se can also influence abiotic conditions. For example, at local scale, forest temperature can be higher at some forest edges, but secondary growth along edges rapidly (<10 years) 'seals' them, reducing the likelihood of edge-interior thermal gradients (reviewed by Arroyo-Rodríguez *et al.* 2017a). In fact, at the landscape scale, fragmentation per se might decrease, not increase air temperature in the landscape. This is so because, fragmentation per se increases the proportion of the matrix that is exposed to cool (and humid) forest interior air (Arroyo-Rodríguez *et al.* (2017a), decreasing air temperature in the matrix through the so-called "vegetation breeze" phenomenon (Cochrane & Laurance 2008). This could lower the land surface temperature at the landscape scale. In fact, in the Brazilian Atlantic forest, the vegetation breeze phenomenon may explain why primary production of forests and sugarcane fields are greater in landscapes with more forest cover (Sousa *et al.* 2019).

Maintenance of water quantity and quality

The critical roles of forest cover in regulating water quantity and quality worldwide is well known (e.g. Calder *et al.* 2007). For example, tropical forests maintain evapotranspiration year-round, whereas evapotranspiration in open matrices such as pastures decreases dramatically in the dry season (Lovejoy & Nobre 2018). As a consequence, longer dry seasons are predicted after deforestation, especially in the Amazon forest, where >40% forest loss can cause significant decreases in rainfall and lengthen the dry season (Sampiao *et al.* 2007). This abiotic change can shift forests to savanna, increase the susceptibility of forests to fires, and negatively impact agriculture in Brazil and adjacent countries (Sampiao *et al.* 2007; Lovejoy & Nobre 2018; Walker *et al.* 2019). Riparian vegetation also regulates watershed hydrological processes, improves water quality, and attenuates floods (Tabacchi *et al.* 2000; Houlahan & Findlay 2010). As riparian forest strips are of particular importance for the provision of these services, they should be considered a high conservation priority in HMFLs (Fig. 1).

Crop pollination, biological pest control and other services

There is increasing evidence that crop pollination and pest control can be enhanced by decreasing the distance from a crop to native forest (reviewed by Grass *et al.* 2019). For example, the proximity of cocoa plantations to old-growth forests in Indonesia increases cocoa productivity by pest control mediated by native forest birds and bats (Maas *et al.* 2013; Linden *et al.* 2019). Similarly, in Costa Rica, insectivorous birds increase in abundance and exert stronger control on borer populations on coffee plantations inserted in more forested landscapes (Karp *et al.* 2013). In Brazil, the maintenance of landscape forest cover is likely to maintain bird and bat predation pressure on cacao herbivores even as agriculture intensifies (Cassano *et al.* 2016). Such pest control is not trivial. For example, predation by insectivorous forest birds on arthropods reduced the infestation of fruits in Jamaican coffee plantations by 1% to 14%, increasing the production value by US$44 to $105/ha (Kellermann *et al.* 2008). On coffee plantations in Costa Rica, pest control by forest birds prevented $75 to $310 ha/year of pest damage (Karp *et al.* 2013). Increasing the number of forest patches in the landscape decreases the distance between crops and forest patches, facilitating the delivery of these important services.

Other important benefits for humans of having both higher forest cover and more biodiversity in the landscape include education/inspiration and aesthetic values (Díaz *et al.* 2006). Also, local people can obtain important economic resources from ecotourism associated with biodiversity, which is an economically significant activity in many locations worldwide (e.g. Serio-Silva 2006). Widespread implementation of integrated landscape-scale approaches will be necessary to reverse global declines in many of the goods and services provided by nature and for achieving sustainable development goals (Reed *et al*. 2016; Diaz *et al.* 2019).

CONCLUSIONS

For decades, ecological studies have proposed different concepts for the management of HMFLs. Our review of these concepts allowed us to propose optimal landscape scenarios for maintaining forest wildlife and delivering goods and services to humans. We emphasize that an optimal landscape should contain at least 40% forest cover, with a higher percentage likely needed in landscapes closer to the equator. Forest cover should be configured so that ~10% occurs in a single (or a few) large forest patch, with the remaining 30% in a large number of evenly-dispersed smaller forest patches. Importantly, the patches should be embedded in a high quality matrix with scattered trees.

Note, however, that we are not suggesting converting the remaining contiguous forests to this "optimal landscape" (Fig. 4 - flow 1). The preservation of extant forests is the top priority (Peres 2005; Gibson *et al.* 2011; Phalan 2018; Edwards *et al.* 2019; Walker *et al.* 2019). Rather, we propose landscape spatial scenarios that can guide conservation and restoration strategies in HMFLs. In particular, we found strong empirical support for the value of increasing (via restoration) as much forest cover as possible (Fig. 4 - flow 2). This is a key conservation priority (Fig. 1). To this end, we should promote the enhancement of farmland yield with biodiversity-friendly methods, such as biological pest control and pollination by native animal species (Phalan 2018; Grass *et al.* 2019). This can be achieved in many agroforestry systems that combine native trees with crops and domestic animals (FAO 2019). When possible, we should also increase landscape heterogeneity by increasing the number/density of forest patches in the landscape and treed elements in the matrix (Fig. 4 - flow 3). Such a spatial configuration can increase connectivity and resource availability at the landscape scale, improving conservation outcomes (Fahrig *et al.* 2019; Fahrig 2020). By maintaining a large percentage (~60%) of landscape area in productive lands, the proposed landscape structure should help to reconcile conservation planning with policymaking, land management, and priorities of local communities. Most of the principles indicated here (e.g. preserving 40% of natural cover, most of it in many small patches) may apply to non-forest ecosystems as well. We hope that the landscape scenarios we propose will motivate future empirical tests of their conservation value and serve as a reference against which other scenarios can be compared.

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Table 1. Suggested management of landscape spatial variables for conservation of forest species based on different ecological concepts.

Attribute	**Suggested management**	**Relevant ecological concepts**	**References**^{a}
Landscape forest cover	Protect and restore as much forest cover as possible	Forest loss vs. fragmentation debate: forest cover generally has stronger (positive) effects on species than forest fragmentation per se	Fahrig (2003, 2017); Watling *et al.* (2020)
		Land sparing/sharing debate: Most forest species, especially those that are incompatible with agriculture, have larger populations if food for people is produced on as small an area as possible, while sparing as large an area of native forest as possible	Phalan (2018); Grass *et al.* (2019)
		Habitat amount hypothesis: species richness in plots of fixed size (species density) is more strongly and positively related to forest cover in the landscape surrounding the plot than to the size of the patch in which the plot is located	Fahrig (2013); Watling *et al.* (2020)
	Preserve or restore at least 40% of forest cover in the landscape	Extinction threshold hypothesis: species generally require 10–30% of habitat (forest) in the landscape for population maintenance	Andrén (1994); Swift & Hannon (2010)
	Minimum forest cover should be higher in landscapes dominated by treeless matrices	Interaction between extinction threshold and matrix quality: the extinction threshold decreases (i.e. more forest cover is needed) with decreasing matrix quality	Fahrig (2001); Swift & Hannon (2010); Boesing *et al.* (2018)
	Minimum forest cover should be higher in landscapes near the equator	Interaction between extinction threshold and species traits: minimum habitat requirements are higher for species with lower reproductive rates, smaller geographic ranges and/or smaller population sizes, which are more commonly found in species near the equator	Swift & Hannon (2010)
		Negative edge effects are stronger in more equatorial regions that have experienced fewer natural disturbances	Betts *et al.* (2019)
Forest fragmentation per se	Preserve most remaining forest (~30% of the landscape) in a large number of small patches, and ~10% in a single very large patch	Fragmentation debate: When significant (<30% of studied cases), most responses to fragmentation per se are mostly positive (75% of significant responses). Crucially, this is independent of the method used to control for forest cover effects, the study taxon, the fragmentation metric used, the response variable, the conservation status of the species, the biome, and the remaining forest cover in the landscape	Fahrig (2017)
		SLOSS (Single Large or Several Small) debate: maintaining a higher number of smaller patches maintains higher gamma diversity than maintaining a lower number of larger patches. Fahrig's (2020) review of SLOSS empirical studies demonstrates that in 63% of SLOSS comparisons there was a difference in species richness between single-large vs. several-small strategies, and of these, 83% demonstrate that several small patches hold more species than a single large patch of the same total area	Simberloff & Abele (1982); Quinn & Harrison (1988); Fahrig (2020)

		Metapopulation theory: fragmentation per se increases the number/density of forest patches and decreases interpatch distances – spatial conditions positively related to metapopulation persistence. This is particularly important in prey (meta)populations, where increasing the number of patches increases opportunities for prey to escape predation in space and time by temporarily building up populations in predator-free patches and then colonizing other patches after predators arrive	Gilpin & Hanski (1991); Wade (1992); Hanski & Ovaskainen (2000)
Vegetation corridors	Preserving and restoring vegetation corridors should be prioritized	Riparian forest strips and semi-natural treed elements in the matrix (e.g. living fences, hedgerows, and single standing trees) can be critical for preserving forest species. They function as ecological corridors, improving ecological connectivity. They also provide important complementary and supplementary resources, including food, water and shelter	Beier & Noss (1998); Tews *et al.* (2004); Harvey *et al.* (2005); Fischer & Lindenmayer (2007); Mitchell et al. (2018); Paoletti et al. (2018); Galán-Acedo *et al.* (2019a)
Matrix quality	Increase tree cover in the matrix	Interacting effects of forest loss and matrix contrast: matrix contrast in forest landscapes decreases with increasing the tree cover in the matrix. This increases the use of the matrix by forest species, decreasing extinction probability with forest loss	Gascon *et al.* (1999); Fahrig (2001); Swift & Hannon (2010); Reider *et al.* (2018); Galán-Acedo *et al.* (2019a)
		Edge effects depend on matrix contrast: negative edge effects increase with increasing matrix contrast (treeless areas in the case of forest)	Harper *et al.* (2005); Arroyo-Rodríguez *et al.* (2017a)
	Increase biodiversity-friendly land cover such as regenerating stands and agroforestry systems	Conservation value of secondary forests: regenerating stands in abandoned lands can help maintain species diversity, tree biomass, and many ecological processes	Chazdon *et al.* (2016); Poorter *et al.* (2016); Arroyo-Rodríguez *et al.* (2017b); Rozendaal *et al.* (2019)
		Land sparing/sharing debate: biodiversity-friendly farming systems (e.g. agroforests) can increase matrix permeability and offer some supplementary resources to some forest species, which can provide important ecosystem services to agriculture (e.g. pollination and pest control)	Perfecto & Vandermeer (2008, 2010); Clough *et al.* (2011); Phalan (2018); Grass *et al.* (2019)
	Implement measures to mitigate the impact of human settlements and infrastructures	Road ecology: roads can directly increase mortality of forest species, limit interpatch movements, facilitate the overexploitation of forest resources, and spread non-native species	Laurance & Peres (2006); Rytwinski & Fahrig (2015); Benítez-López *et al.* (2019); Osuri *et al.* (2020)
		Environmental education and enforcement: Environmental education and enforcement of regulations increase public awareness and knowledge about natural forests and threats, such as illegal hunting and trade, and can promote the sustainable use of forest products and the development of biodiversity-friendly economic activities such as ecotourism	May (2010)

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[a] Only some key reviews and meta-analysis are included. Additional supporting references are included in the main text.

Box 1. Defining relevant land management variables

Different landscape metrics show different effects of landscape structure on forest species. Therefore, evaluating their relative impact is needed to guide management strategies (Fahrig 2003; Watling *et al.* 2011). This is, however, challenging because >100 metrics have been proposed for measuring landscape structure. These metrics can be classified in two groups, those describing landscape composition and those describing landscape configuration (McGarigal *et al.* 2012). Landscape composition refers to the types of land cover (e.g. forest, pasture) and the amounts of the different cover types in the landscape. Landscape configuration refers to the spatial arrangement or physiognomy of the cover types (Fahrig *et al.* 2011). For instance, the percentage of the landscape covered by forest and the richness of land cover types in the landscape are typical metrics of landscape composition, whereas the number of forest patches and mean patch size are typical metrics of landscape configuration.

Another important challenge when assessing landscape variables is that they often co-vary with one another. Of particular concern are relationships between forest amount and several configuration metrics (Fahrig 2003). For example, mean patch size and isolation are often considered configuration metrics, but they are strongly correlated with total forest cover, and so they can also be considered composition metrics (Fahrig 2003). In addition, metrics of forest fragmentation such as the number or density of forest patches typically have a unimodal relationship with forest loss (Fahrig 2003; Villard & Metzger 2014; Taubert *et al.* 2018). Thus, measurements of fragmentation per se, in which the effect of forest loss is experimentally or statistically controlled (Fahrig 1999, 2003), most accurately describe configuration effects on biodiversity.

The composition and configuration of non-forest land cover in the landscape (here referred to as the matrix) can also be of key relevance for forest species. In fact, there is a gradient from low-quality matrix where mortality of forest species is very high, to high-quality matrix where survival of forest species is high. A high-quality matrix (e.g. arboreal crops, agroforestry systems) often contains resources (Perfecto & Vandermeer 2008, 2010; Harvey *et al.* 2005, 2006; Asensio *et al.* 2009; Prevedello & Vieira 2010; Driscoll *et al.* 2013; Mendenhall *et al.* 2016; Ferreira *et al.* 2018; Galán-Acedo *et al.* 2019a; Frishkoff *et al.* 2019), facilitates successful movement between forest patches (Uezu *et al.* 2008; Galán-Acedo *et al.* 2019a), and buffers negative edge effects by decreasing forest-matrix contrast (Mesquita *et al.* 1999; Harper *et al.* 2005; Arroyo-Rodríguez *et al.* 2017a). In contrast, low-quality matrix (e.g. roads, annual crops) generally threatens forest species by: (i) increasing mortality of dispersing individuals, e.g. by roadkill (Fahrig *et al.* 1995; Fahrig & Rytwinski 2009) and pesticides (Sánchez-Bayo & Wyckhuys 2019); (ii) generating substantially drier and warmer microclimates than in forest (Nowakowski *et al.* 2018a, 2018b); (iii) increasing predation risk by feral animals (May & Norton 1996); and (iv) facilitating the invasion and spread of exotic species (Hobbs 2001; Rutt *et al.* 2019). Some matrix types even can function as ecological traps for forest animals, thus reducing population persistence (Battin 2004). Therefore, considering matrix quality is critical to designing biodiversity-friendly landscapes.

Two important perspectives on matrix management that have direct implications on the remaining landscape forest cover are the "land sparing" and "land sharing" approaches (Perfecto & Vandermeer 2010; Phalan 2018). Land sparing implies "increasing of yields on farmed land while at the same time protecting native vegetation or freeing up land for habitat restoration elsewhere", whereas land sharing entails "producing both food and wildlife in the same parts of the landscape by maintaining or restoring the conservation value of the farmed land itself" (Phalan 2018). Thus, land sparing proposes decreasing the total landscape area under production to increase the area for conservation or restoration, whereas land sharing focuses on minimizing the impact of agriculture on in-farm biodiversity, although this strategy may decrease agricultural yields, potentially limiting the landscape area available for conservation.

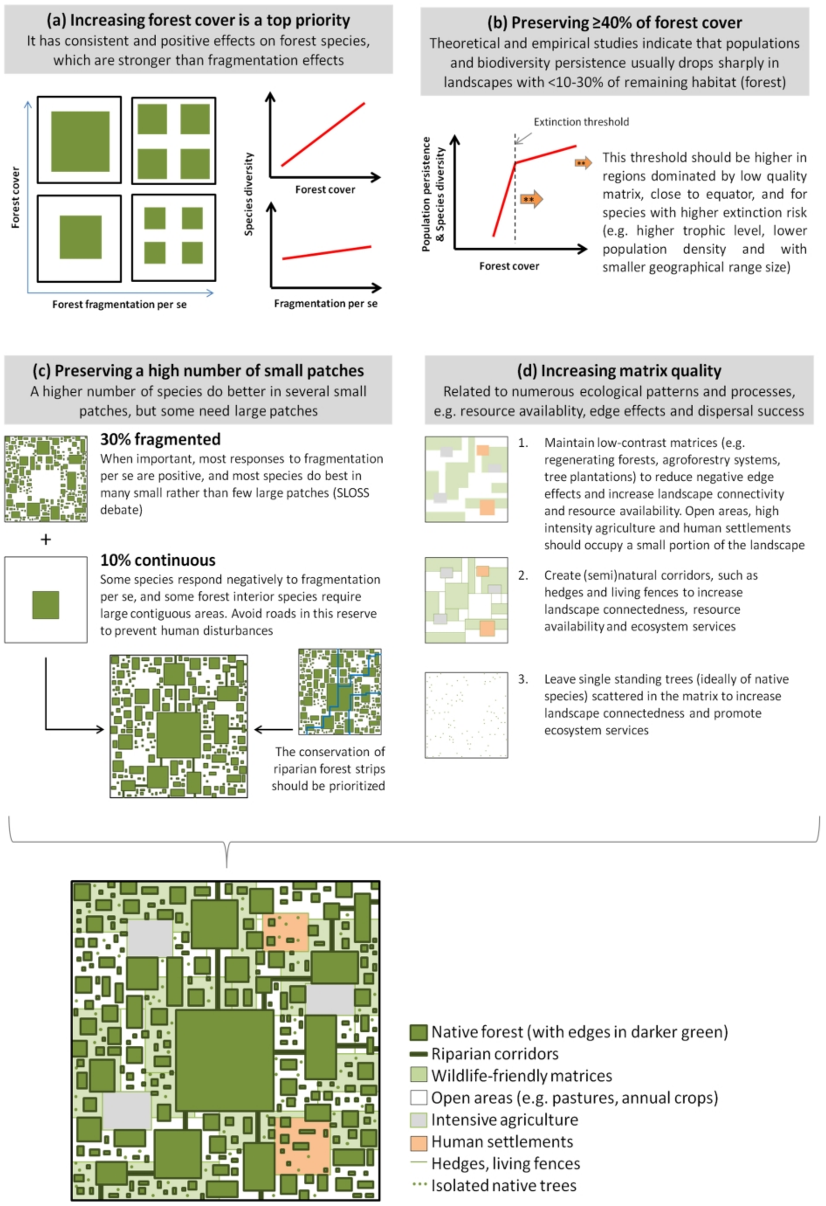

Figure 1. Schematic of optimal landscape spatial scenarios for preserving forest wildlife. Increasing forest cover is a top priority (a). An optimal landscape should contain ≥40% forest cover, but higher percentages are likely needed in landscapes with low quality matrix and closer to the equator (b). This forest cover should be configured so that ~10% occurs in a single large forest patch, with the remaining 30% in a large number of evenly-dispersed smaller forest patches (c). Vegetation corridors are of very high conservation value, especially riparian corridors, as they can increase connectivity in treeless matrices (c). The landscape needs to be sufficiently large (e.g. several thousands of square kilometers) that 10% of its area meets minimum area requirements for species that do better in large, contiguous patches. Importantly, the patches should be embedded in a high quality matrix with scattered trees, and farms should be delimited by semi-natural treed elements (d). Although evidence supports that most remaining forest should be preserved in a large number of small patches, we include different patch sizes to simulate the distribution of patch size in some ‘real-world’ landscape scenarios (Taubert et al. 2018). Note that some open areas (e.g. pastures, annual crops) and human settlements have forest patches and dispersed trees to make them more biodiversity friendly. Yet, we also include some intensified (treeless) open areas to indicate intensive farming

systems. These farms should occupy a small extent because of the high yields they offer and the damage they cause to forest species (Hendershot et al. 2020). All farms are delimited by semi-natural treed elements, and all wildlife-friendly matrices (e.g. agrosilvicultural systems, silvopastoral systems, and agrosilvopastoral systems) have isolated native trees. For clarity, we do not include roads, but we should avoid roads in reserves and larger patches to prevent human disturbances.

508x744mm (144 x 144 DPI)

Figure 2. Example of a biodiversity-friendly forest landscape from Las Alturas de Cotón, Puntarenas, Costa Rica. The remaining tropical forest (right side) is part of the La Amistad International Peace Park, which protects widely diverse habitats, including tropical lowland rainforest and cloud forests. This 401,000 ha park maintains a very well preserved flora and fauna, and is surrounded by different-sized forest patches and a high-quality matrix with semi-natural elements, such as riparian corridors, living fences and dispersed native trees.

508x285mm (96 x 96 DPI)

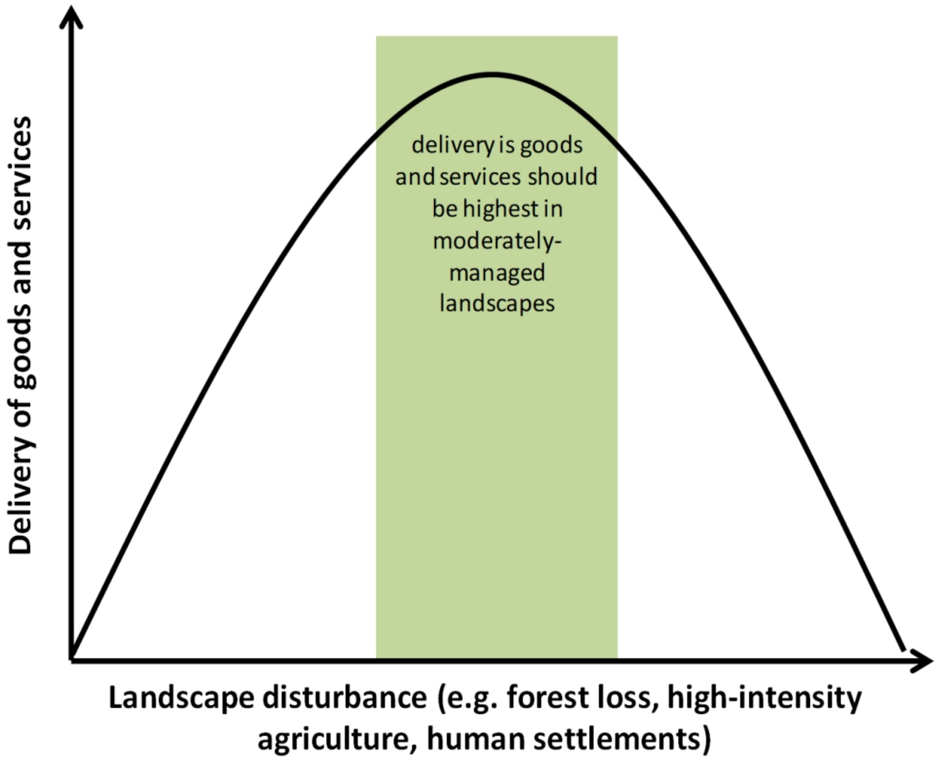

Figure 3. Goods (e.g. timber, firewood, meat) and ecosystem services (e.g. carbon storage, soil protection, water cycling) are positively correlated with forest aboveground biomass (Balvanera et al. 2006). Therefore, delivery of goods and services is expected to increase with increasing use of forest resources by humans. Yet, there should be a point beyond which increasing forest disturbance decreases the amount and quality of forest resources in the landscape, limiting the delivery of goods and services. This implies that the maximum level of goods and services should be obtained at moderate levels of disturbance, as the landscape scenario proposed here. Modified from Melo et al. (2013).

259x219mm (144 x 144 DPI)

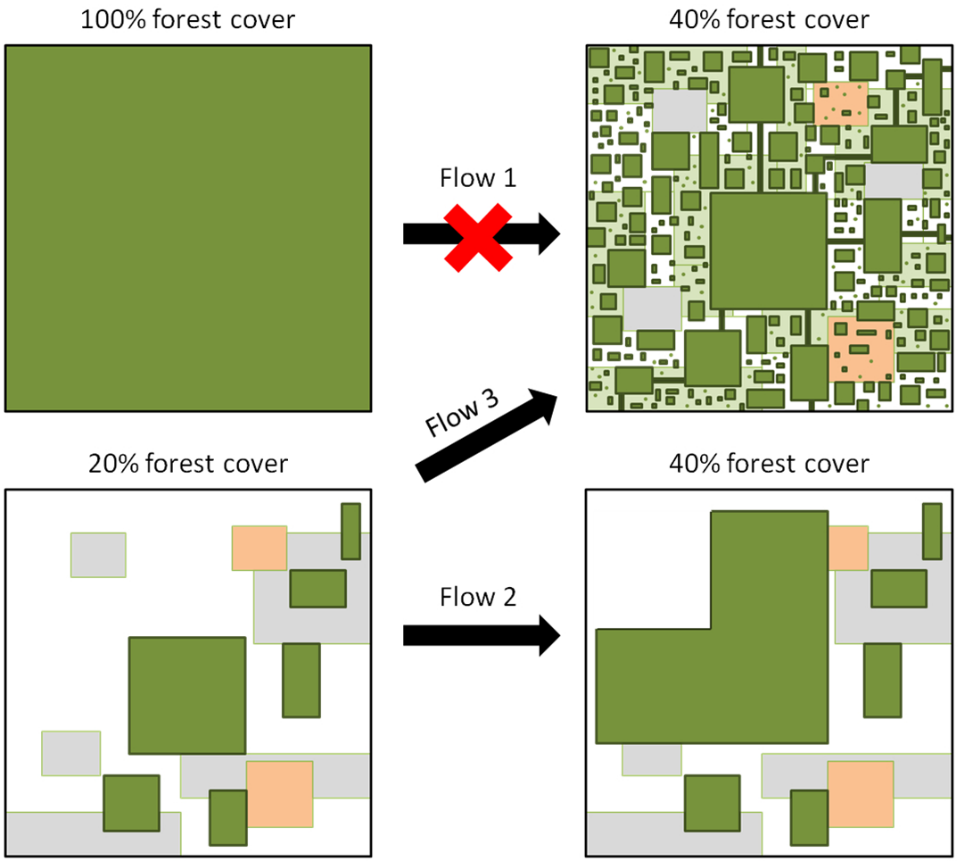

Figure 4. Contrasting land-use changes in human-modified forest landscapes. Large forested areas should not be converted to fragmented forest landscapes (Flow 1). We rather suggest several management strategies to restore largely deforested landscapes. Increasing forest cover should be a top priority (Flow 2). Yet, such increases will promote more effective conservation outcomes if focused on a higher number of smaller forest patches, including riparian corridors and semi-natural treed elements dispersed in an agricultural matrix of higher quality (Flow 3).

296x265mm (96 x 96 DPI)