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REVIEW

Beyond the fragmentation debate: a conceptual model to predict when habitat configuration really matters

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Summary

1. Research addressing the effects of habitat fragmentation on species, assemblages or ecosystems has been fraught with difficulties, from its conceptual foundation to statistical analyses and interpretation. Yet, it is critical to address such challenges as ecosystems are rapidly being altered across the world.

2. Many studies have concluded that effects of habitat loss exceed those of fragmentation *per se*, that is, the degree to which a given amount of habitat is broken apart. There is also evidence from different biomes and taxa that habitat configuration, that is, the spatial arrangement of habitat at a given time, may influence several landscape processes such as functional connectivity, edge and matrix effects, and thus population viability.

3. Instead of focusing attention on the relative influence of either habitat loss or fragmentation, we must identify portions of the gradient in habitat amount where configuration effects are most likely to be observed. Here, we suggest that all species are, to a certain degree, sensitive to landscape change and that, assuming a homogeneous matrix, habitat configuration will have a higher influence on species at intermediate values of habitat amount, where configuration has potentially the greatest variability.

4. On the basis of empirical studies and simulations, we expect that species that are relatively tolerant to fragmentation of their habitat will exhibit a wider band where amount and configuration interact compared to species less tolerant to fragmentation.

5. *Synthesis and applications*. Reducing habitat loss should be a top priority for conservation planners. However, researchers should also investigate the indirect impacts of habitat loss on biodiversity through fragmentation effects. This research aims to identify windows of opportunity where habitat configuration can mitigate to some extent the effects of habitat loss, particularly through the maintenance of functional connectivity.

Key-words: dispersal, fragmentation threshold, functional connectivity, habitat availability, land use intensification, matrix, movement ecology, reachability

Introduction

The long-standing debate on the relative influence of habitat loss versus fragmentation seems to have arrived at a cross-roads. Although the two phenomena occur simultaneously in many circumstances (Haila 2002) and their effects are often confounded (Smith *et al.* 2009; Didham, Kapos & Ewers 2012), several authors have stressed the importance of isolating the effects of these two phenomena (Fahrig 2003; Lindenmayer & Fischer 2007) and pointed out the prominence of the effects of habitat loss over those of habitat fragmentation (Fahrig 2003; Mortelliti *et al.* 2011; Smith, Fahrig & Francis 2011). However, many field experiments indicate that the configuration of both habitat (Bélisle & Desrochers 2002; Robertson & Radford 2009) and matrix (Aben *et al.* 2012; Villard & Haché 2012) strongly influence landscape permeability, as well as species interactions (Roland 1993; Cooper, Li & Montagnes 2011).

The Manichaean perspective often conveyed by the habitat loss versus fragmentation debate has slowed research progress to stem the biodiversity crisis at a time when land use change (Gibson *et al.* 2011; Lindenmayer,

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Cunningham & Young 2012) and climatic change (Rosensweig *et al.* 2008) are rapidly altering ecosystems. Indeed, most indicators suggest that threats to biodiversity are not slowing down (Butchart *et al.* 2010). Stemming habitat loss should remain a top priority for conservation, but the spatial pattern of habitat loss also requires attention from researchers because we cannot ignore finer-scale effects of habitat configuration as well as those of matrix composition on functional connectivity, and their ultimate outcome for population persistence and ecological integrity.

Inconsistent use of terminology has muddled a debate that is already complex by its very nature, so we wanted to make sure that the conceptual basis of this paper would be clear. First, we refer to fragmentation as the process through which the habitat of a focal species is 'broken apart' (Fahrig 2003) by the creation of land cover types, collectively referred to as the matrix, that are generally unsuitable for reproduction and more or less permeable to movements of the focal species compared to the focal habitat. The spatial arrangement of habitat at a given time, which results from past habitat loss and fragmentation, is called habitat configuration. Habitat configuration will, in turn, influence functional connectivity, defined here as the movement rate of individuals across the landscape, considering inter- and intrapatch movement (Pascual-Hortal & Saura 2006). Taken more broadly, functional connectivity reflects the interaction of a species' movement ability and landscape structure, that is, all habitat and matrix types present (landscape composition) and their spatial arrangement (landscape configuration) (Fig. 1).

Challenges facing fragmentation research

Disentangling the effects of habitat amount, configuration and matrix composition on biota is especially challenging for at least five reasons: (i) most if not all configuration metrics covary with habitat amount (Fahrig 2003 and references therein), thus challenging the distinction of their independent effects; (ii) fragmentation effects may be restricted to the lower (Andrén 1994; Radford, Bennett & Cheers 2005; Betts *et al.* 2006) or middle (Pardini *et al.* 2010; Martensen *et al.* 2012) portions of the gradient in habitat amount, further complicating their detectability; (iii) landscape units with similar habitat amounts but varying configurations are uncommon in the real world, especially for a given matrix type (e.g. Gobeil & Villard 2002; but see McGarigal & McComb 1995; Robichaud, Villard & Machtans 2002; Prist, Michalski & Metzger 2012); (iv) biological responses to changes in landscape structure are complex and not always easy to detect because they may vary among species or functional groups (Van Houtan *et al.* 2007; Vetter *et al.* 2011), matrix type (Prevedello & Vieira 2010), geographic locations (Baldi 1996; Lindell *et al.* 2007; Betts & Villard 2009), spatial extents (Deconchat, Brockerhoff & Barbaro 2009; Smith, Fahrig & Francis 2011; Banks-Leite, Ewers & Metzger 2013) or as a function of time since fragmentation (Petit & Burel 1998; Lindborg & Eriksson 2004; Callens *et al.* 2011).

Not surprisingly, then, the numerous attempts to detect consistent patterns in the responses of different species, guilds or functional groups to fragmentation of their habitat (e.g. Debinski & Holt 2000; Henle *et al.* 2004; Lampila,

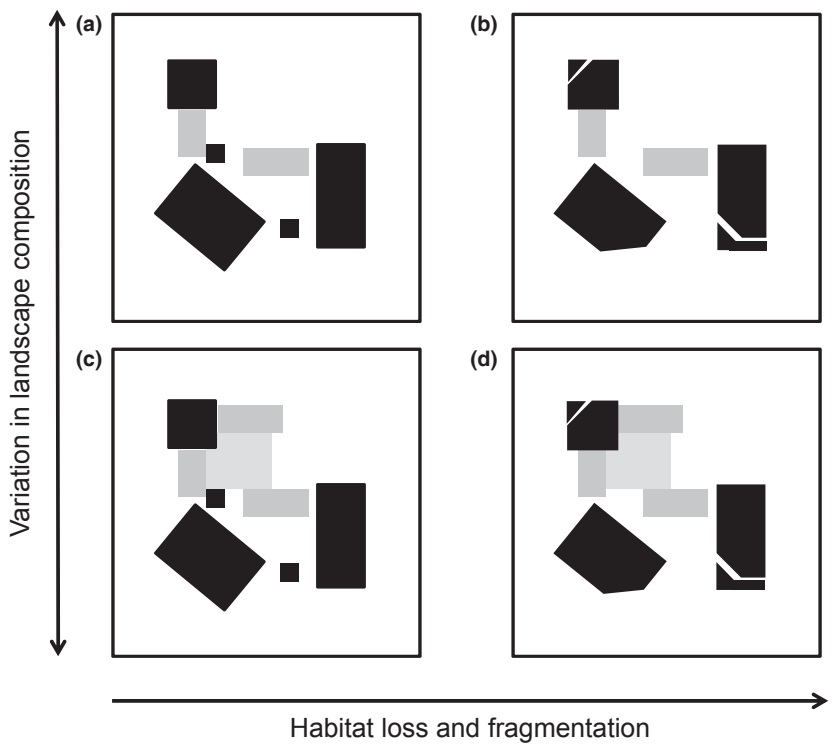

Fig. 1. Schematic example of changes in landscape structure associated with loss and fragmentation of a focal habitat type (in black), as well as shifts in matrix composition (white and grey tones). Changes from landscapes (a) to (c) and (b) to (d) pertain to landscape composition, without alteration of the configuration (spatial arrangement) of the focal habitat. Changes from landscapes (a) to (b) and (c) to (d) alter habitat (and landscape) configuration. Changes in landscape structure may in turn affect landscape permeability to movements of organisms.

Mönkkönen & Desrochers 2005; Vetter *et al*. 2011; Banks-Leite, Ewers & Metzger 2012) have tended to yield few generalizations.

Habitat loss, habitat fragmentation and ecological research

Habitat being a species-specific concept, the occurrence and abundance of all species should increase with habitat amount, each fragment becoming more accessible as habitat becomes increasingly connected (Boscolo *et al*. 2008; Awade, Boscolo & Metzger 2012) and approaches the percolation threshold (King & With 2002). The pool of immigrants also increases with habitat amount (Venier & Fahrig 1998; Betts & Villard 2009; Hadley & Betts 2012). Greater habitat amount may also (indirectly) mitigate some detrimental effects of the matrix or proximity to edges. Hence, habitat amount *per se*, and steps to maintain or increase it, should be a priority for conservation planning. The indirect effects of habitat amount on functional connectivity and matrix and/or edge effects still require detailed scientific investigation.

There is theoretical and empirical evidence from metapopulation models (e.g. the incidence function; Hanski & Gilpin 1997) and other spatially explicit modelling approaches (e.g. Fahrig 1998; Rubio & Saura 2012) that different configurations of a given amount of habitat can affect functional connectivity or species persistence (Fahrig 1998), at least over certain portions of the gradient in habitat amount (Fig. 2). Several authors have suggested that habitat configuration is particularly significant below a certain amount called the 'fragmentation threshold', usually around 10–30% (Andrén 1994; Fahrig 1997; Betts *et al*. 2006). In landscapes where habitat amount is high enough to meet the requirements of species of conservation concern, but insufficient to allow extensive movement, research could make critical contributions to identify priority interventions to maintain or restore functional connectivity (e.g. Epps *et al*. 2005; Proctor *et al*. 2005; Pardini *et al*. 2010; Desrochers *et al*. 2011). Research is also critically needed to understand the mechanisms underlying the negative effects of certain matrix types on habitat quality (Robinson *et al*. 1995; Banks-Leite, Ewers & Metzger 2010; Falk, Nol & Burke 2011; Poulin & Villard 2011) and permeability to the movements of certain taxa (Kennedy & Marra 2010; Villard & Haché 2012), as well as to identify drivers of habitat degradation (Laurance *et al*. 2002; Pérot & Villard 2009; Knowlton & Graham 2011). Thus, habitat amount is always an important consideration, whereas habitat configuration (or more broadly, landscape structure) has the potential to reduce or mitigate the effects of habitat loss.

The non-trivial implications of fragmentation

Although habitat fragmentation often takes place through large-scale habitat conversion by agriculture, residential development, mining or other anthropogenic land uses, changes in habitat configuration may also result from minor habitat gain or loss. For example, in landscapes

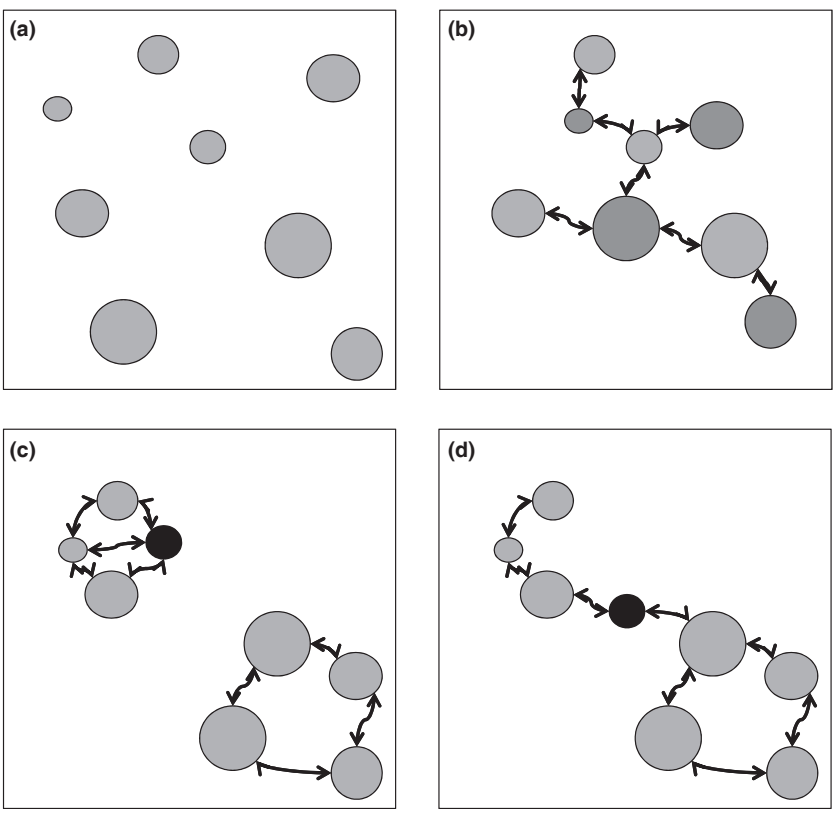

Fig. 2. The spatial arrangement of habitat patches matters. Landscapes with the same amount of habitat and also with the same number of patches of the same size, but in different spatial locations, may result in situations where functional connectivity and habitat reachability are completely different for a hypothetical species. In scenario (a), patches are too isolated and there are no biological fluxes among them (similar to a 'metapopulation in non-equilibrium'), while in scenario (b), the displacement of four patches allows free movement among all patches (like in a 'patchy metapopulation'). In scenarios (c) and (d), the insertion (or restoration) of a small patch (in black) in different locations may have very different effects on functional connectivity and the corresponding habitat network.

where habitat is sparse from the perspective of a given species, ecological restoration may significantly increase interpatch connectivity through the addition of small patches or linear elements (Fischer & Lindenmayer 2002; Lloyd & Marsden 2011). In contrast, when habitat amount and structural connectivity are high, roads may significantly reduce interpatch connectivity and population abundance of certain species (Merriam *et al.* 1989; Develey & Stouffer 2001; Dyer *et al.* 2001; Gravel, Mazerolle & Villard 2012) through barrier effects or increased mortality (Rytwinski & Fahrig 2012) and, in some cases, isolate their populations (Epps *et al.* 2005; Proctor *et al.* 2005; Lesbarrères *et al.* 2006; Clark *et al.* 2010), despite the fact that the total area disturbed is modest at a landscape scale. Thus, considering how landscape configuration can influence functional connectivity in fragmented landscapes may be especially insightful to optimize conservation actions. Indeed, different options to add a given amount of habitat can have drastically different outcomes for taxa whose movement ability is restricted for physical or behavioural reasons (Fig. 2). Hence, for a given amount of habitat, it is important to predict configurations resulting in higher functional connectivity and, thus, a higher probability of persistence. Interestingly, adding habitat patches or linear elements to restore functional connectivity will be interpreted through many configuration metrics as a slight increase in fragmentation. In this context, habitat availability or reachability (Pascual-Hortal & Saura 2006; Saura & Rubio 2010) is a useful measurement of functional connectivity because it allows joint consideration of the effects of habitat amount and spatial pattern (and connectivity) on the persistence of focal species.

A conceptual model to integrate habitat amount and configuration

Data from real landscapes (Oliveira Filho & Metzger 2006; for example) and from simulations in neutral landscapes indicate that variability in fragmentation metrics (number of patches, total length of edge) is higher at intermediate values of habitat amount (Fig. 3). When considering an index of habitat availability or reachability (ECA(IIC), calculated using Conefor 2.6; Saura & Torné 2012), variability increased in the middle portion of the gradient in habitat amount (Fig. 4). When habitat amount was held constant, this index decreased with fragmentation, irrespective of the movement ability, and the highest variability in reachability index was also observed at an intermediate amount of habitat (45–50%; Fig. 5).

Taken together, these results suggest that it is statistically more likely that habitat configuration will influence animal movements across the landscape and species persistence at intermediate values along the gradient in habitat amount. According to the fragmentation threshold hypothesis, one would expect to observe a stronger effect of configuration at the low end of the gradient in habitat amount. However, the low variability of habitat configuration when habitat amount is low, and the interspecific variability in the range of habitat amounts over which configuration matters might explain the paucity of empirical evidence for fragmentation thresholds (Swift & Hannon 2010). Additionally, the reasoning developed by Tscharntke *et al.* (2012) according to which conservation actions at intermediate landscape complexity levels are more effective can theoretically be applied to configuration effects. In other words, the effects of landscape management or

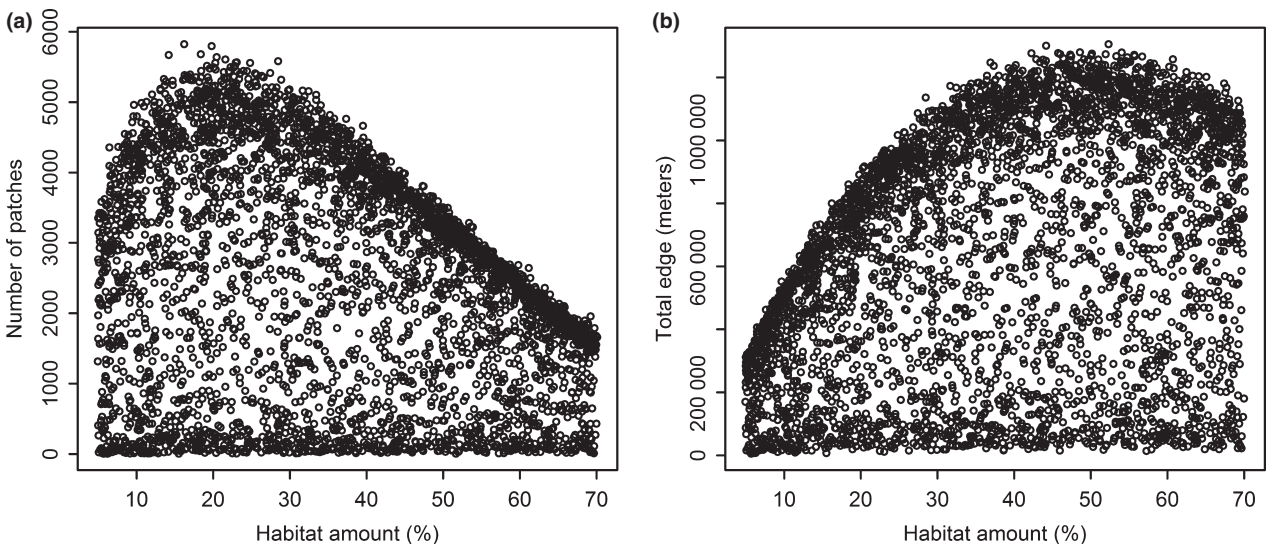

Fig. 3. Relationship between habitat amount and its configuration (number of patches; total length of edge) for 4000 simulated landscapes varying in habitat amount (5–70%) and aggregation level obtained with QRule software (Gardner & Urban 2007). Each landscape has 512 × 512 pixels, which represents 23 592·96 ha for a 30-m pixel size. At intermediate habitat amounts, landscapes show higher variability in habitat fragmentation indices, around 20% of habitat amount for number of patches (a) and 50% for total edge (b). Variability tended to decrease for lower values of habitat amount.

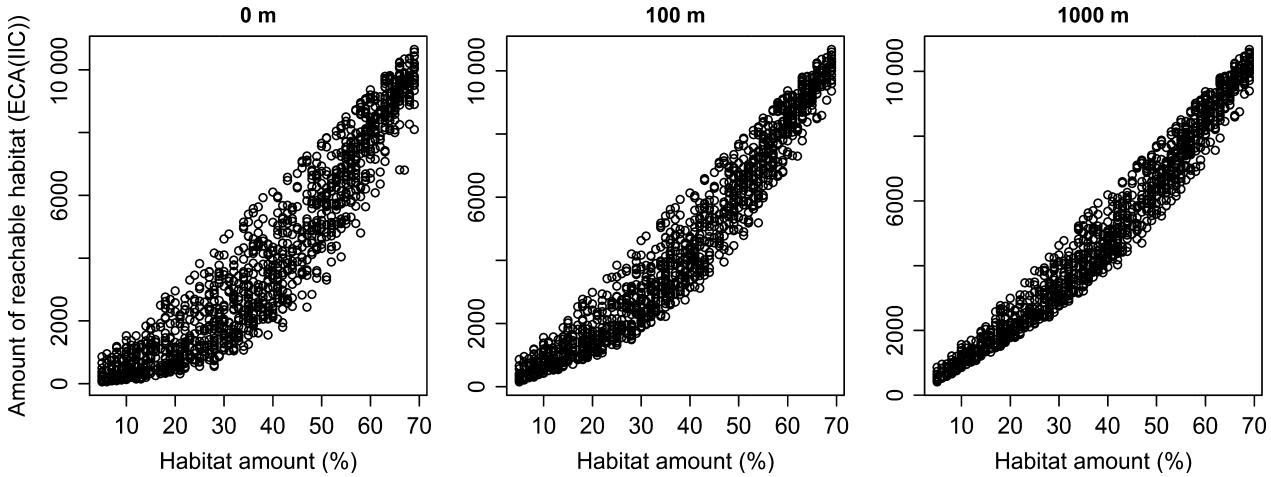

Fig. 4. Variation in habitat availability (ECA(IIC); in hectares) as a function of habitat amount in the landscape for three levels of species dispersal ability (0, 100, 1000 m) considering the same landscapes presented in Fig. 3. The integral index of connectivity (IIC) is a graph-based index that represents habitat availability for a species considering the habitat spatial arrangement and the species dispersal ability. The equivalent connected area (ECA) of the IIC represents the size that a single habitat patch (maximally connected) should have in order to provide the same value of IIC than the actual habitat pattern in the landscape (Saura *et al.* 2011). The larger the value, the larger the amount of reachable habitat.

configuration on species richness should be lower when beta diversity is low, that is, when alpha diversity is homogeneously low (low forest cover; generalist species dominant) or high (high forest cover; specialist species dominant). When forest cover (or landscape complexity) is intermediate, then beta diversity would be expected to be higher (coexistence of generalist and specialist species), and relatively minor changes in habitat configuration can substantially modify biological fluxes, impeding or facilitating movement among patches after fragmentation or habitat restoration, respectively. All those arguments support the idea that strongest effects of configuration should be observable at the middle range of habitat amount.

Within species, evidence for interaction effects between habitat amount and configuration is equivocal. Studies investigating such interactions are rare and have either

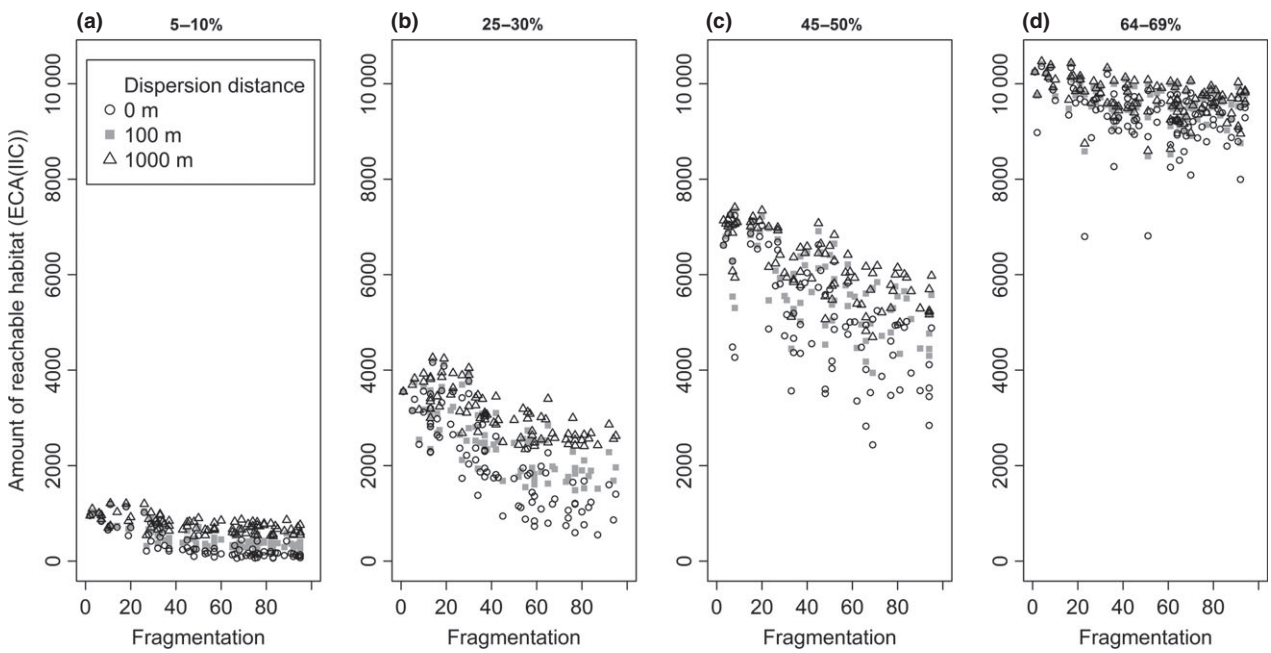

Fig. 5. Variation in habitat availability (ECA(IIC); in hectares) as a function of habitat fragmentation (the inverse value of aggregation index from QRule: 1-H), for different ranges of habitat amount (a, b, c, d) and for three levels of dispersal ability (0, 100 and 1000 m). Simulated landscapes are the same as in Fig. 3. Note that habitat amount is maintained essentially constant in each subgraph. See Fig. 4 for an explanation of ECA(IIC).

been based on relatively coarse response variables (e.g. Trzcinski, Fahrig & Merriam 1999) or a small number of species (e.g. Betts *et al*. 2006; Mortelliti *et al*. 2011; Smith, Fahrig & Francis 2011). However, we have recent and strong evidence from an Atlantic forest project that configuration can affect more strongly species abundance and richness at intermediate amounts of habitat (30%), when compared with landscapes with 10 and 50% of habitat left. This was observed in small mammals (Pardini *et al*. 2010), birds (Martensen *et al*. 2012), and amphibians (M. Dixo, T.H. Condé & R.T. Bruscagin, unpublished data). There is also other scattered empirical evidence that structural connectivity, in the form of hedgerow networks (Mortelliti *et al*. 2011) and stepping stones (Uezu, Beyer & Metzger 2008), has the greatest influence on species in landscapes with intermediate habitat cover. Nonetheless, further empirical studies addressing this issue are in dire need.

Finding minimal or critical values of habitat amount is already a challenge in itself, which has been systematically pursued using different theoretical backgrounds such as the island biogeography theory (e.g. minimum habitat requirements), population demography and genetics (e.g. area supporting a 'minimum viable population'), or metapopulation theory (e.g. 'metapopulation capacity'; Hanski & Ovaskainen 2002). However, if habitat amount is strongly related to habitat configuration (e.g. Neel, McGarigal & Cushman 2004) and the matrix is homogeneous, it follows that minimum habitat requirements for population persistence will be influenced by habitat configuration and that they will be higher when configuration impedes functional connectivity or reduces habitat reachability (Fig. 6a). Hence, we hypothesize that a specific portion of the gradient in habitat amount will be characterized by the interaction of habitat amount and configuration effects on species persistence and that above that portion, only habitat loss will matter (Fig. 6a). This region where habitat amount and configuration interact is situated between the 'extinction threshold' and the 'fragmentation threshold' (Fahrig 2003; Fig. 6a). Minimum habitat requirements can be higher or lower according to a species' sensitivity to habitat loss, thus influencing the specific location along the gradient where regional extirpation will be expected (Fig. 6b). Furthermore, depending on life-history characteristics of species, the width of the interacting region will also vary (Fig. 6b). Specifically, the relative tolerance of a species to changes in habitat configuration may restrict or expand the range of habitat amount over which it can occur.

The literature is replete with examples of species' sensitivity to habitat loss (e.g. Edman *et al*. 2004; Homan, Windmiller & Reed 2004; Develey & Metzger 2006; Betts, Forbes & Diamond 2007). However, research is needed to better understand the relative tolerance of different species to changes in habitat configuration. According to our conceptual model, a species that is tolerant to habitat configuration should respond over a wider range of habitat amount, persisting in landscapes with favourable configurations

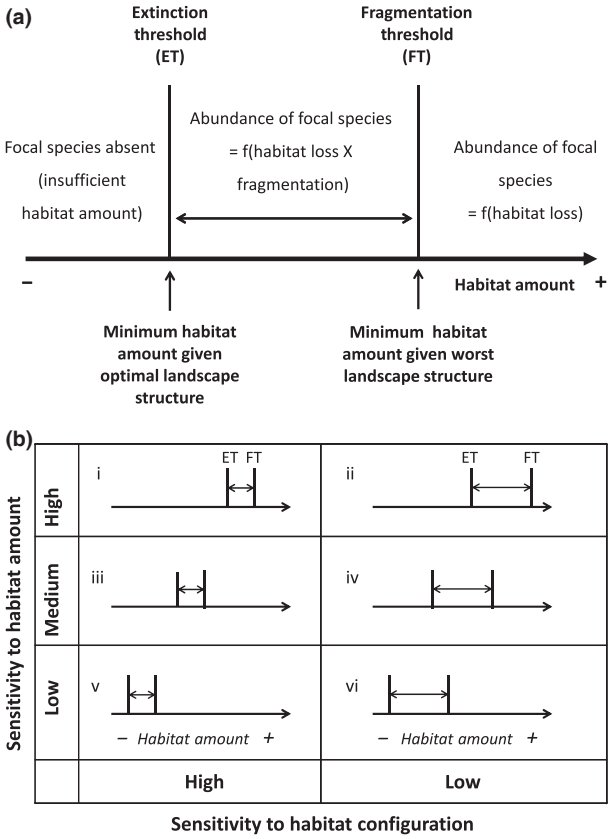

Fig. 6. Theoretically, the minimum habitat amount required by each species to persist depends on some landscape characteristics, such as matrix composition and the spatial arrangement of habitat, which can both influence habitat reachability. When landscape structure is more favourable to movements, species may require a smaller area of habitat. Hence, species occurrence and abundance may be regulated at the same time by habitat loss and fragmentation in the mid-portion of the gradient in habitat amount, whereas only habitat loss will matter when habitat amount is high (above the 'fragmentation threshold' – FT) and the species will not persist when this amount falls below a threshold (the 'extinction threshold' – ET) (a). This general framework can help to distinguish different species profiles (i to vi) according to their tolerance to habitat configuration and habitat amount (b).

when habitat amount is low (Fig. 6). The white-shouldered fire-eye *Pyriglena leucoptera* Vieillot is a good example of this phenomenon. This understorey bird species from the Brazilian Atlantic forest occupies landscapes featuring a wide range of habitat amount (e.g. 10–100%) and is influenced by configuration in landscapes with 10–50% habitat (Martensen *et al*. 2012). At the lower end of this range, this species occurs in landscapes whose fragments are either large enough to accommodate a breeding pair or close enough to allow functional connectivity (i.e. landscape supplementation: Dunning, Danielson & Pulliam 1992; Villard, Merriam & Maurer 1995; Martensen, Pimentel & Metzger 2008; Boscolo & Metzger 2011; Banks-Leite, Ewers & Metzger 2012). In more forested landscapes, with up to 50% habitat, the white-shouldered fire-eye can occupy smaller and more isolated patches (Banks-Leite, Ewers &

Metzger 2012). A similar pattern can be found in the scarlet tanager *Piranga olivacea* Gmelin, a Nearctic–Neotropical migrant bird species that occupies landscapes representing a broad range of habitat amounts (10–100%), but still responds to fine-scale habitat configuration (Villard, Merriam & Maurer 1995; Villard, Trzcinski & Merriam 1999; Hames *et al*. 2001). Fraser & Stutchbury (2004) have shown that this species can move frequently among small, spatially aggregated fragments, combining them into its territory.

Species that are more sensitive to habitat configuration are expected to respond to this property over a narrower range of habitat amount and will generally depend more strongly on local habitat quality or have a low ability to move across the matrix, in spite of their large area requirements. For example, the white-browed foliage-gleaner *Anabacerthia amaurotis* Temminck, a red-listed understorey bird species, breeds in pristine unbroken Atlantic forest but also occurs in unbroken second-growth forest, albeit at lower abundance, and in fragmented landscapes with ca. 50% habitat, where it is restricted to the larger fragments (Banks-Leite, Ewers & Metzger 2012). This species would be classified in profile 'i' in Fig. 6b.

This conceptual model raises two specific predictions: (i) extinction thresholds for a given species will vary as a function of habitat configuration and (ii) configuration will no longer matter above a certain amount of habitat. Those predictions could be tested by comparing extinction thresholds for a given species in landscapes where the spatial pattern of habitat loss created different configurations (e.g. more or less aggregated; see Oliveira Filho & Metzger 2006 for an example) and by comparing the effects of configuration at different levels of habitat amount. Testing those predictions and the hypothesis of significant effects of habitat configuration at intermediate levels of habitat amount will require true landscape-level or land-mosaic studies (sensu Bennett, Radford & Haslem 2006), with replication so that species responses can be compared across gradients in habitat amount and configuration.

A window of opportunity for conservation

We reiterate that minimizing habitat loss should be the priority for biodiversity conservation. This is especially true for species that cannot persist in the absence of very large tracts of undisturbed habitat (e.g. primary forests – Develey & Metzger 2006; Barlow *et al*. 2007a; Callens *et al*. 2011; Gibson *et al*. 2011). Nonetheless, a significant number of species can also persist in fragmented landscapes, and for those species, there is a broad spectrum of options for conservation action. Managing habitat quality, habitat configuration and matrix composition may represent valuable alternatives to maintain a species in landscapes where a significant increase in habitat amount is impossible over the short term (Fig. 7). However,

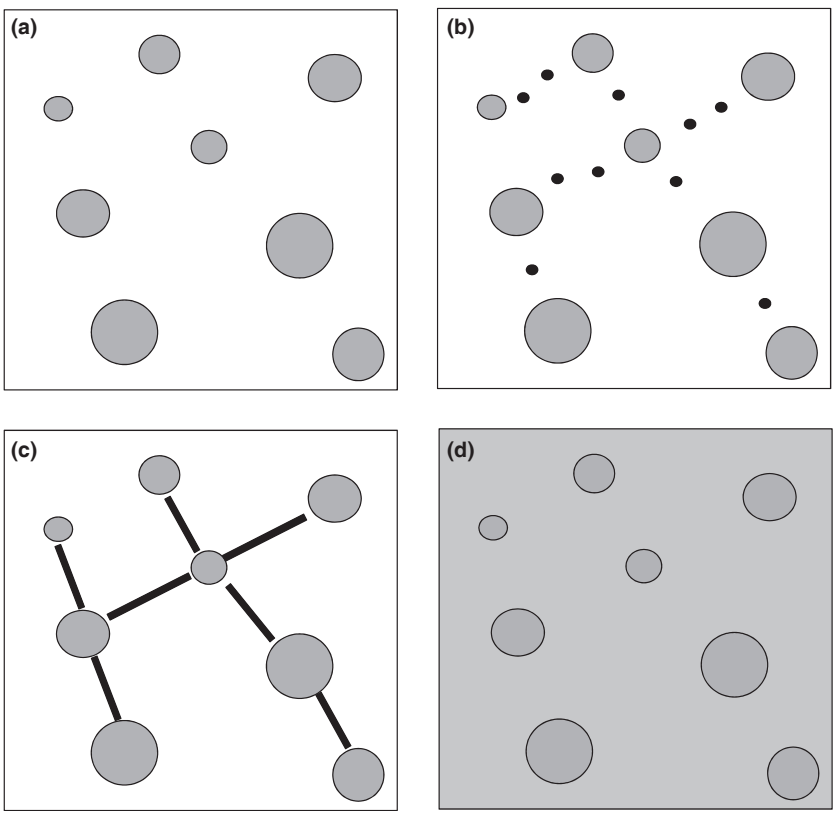

Fig. 7. Examples of how habitat configuration and matrix composition may have profound effects on functional connectivity. Considering a reference situation (a), the creation of stepping stones (b), thin corridors (c) or the improvement of matrix permeability (d) may all result in an increase in functional connectivity among previously isolated habitat patches.

research is needed to identify trade-offs between those landscape management options.

Thus far, research has shown that scattered trees or small patches acting as stepping stones for movements may increase functional connectivity (Fischer & Lindenmayer 2002; van der Ree, Bennett & Gilmore 2004; Leidner & Haddad 2011; Lloyd & Marsden 2011). Linear landscape elements ('corridors') may also enhance movements across relatively impermeable matrices (Robichaud, Villard & Machtans 2002; Tewksbury *et al.* 2002). Finally, matrix management may offer creative options for facilitating movements of organisms through different processes (emigration from a home patch, immigration into a new habitat patch and inter-patch movements; Bowler & Benton 2005). Despite the challenge of quantifying matrix permeability because it may vary spatially (Kennedy & Marra 2010; Villard & Haché 2012) and temporally (e.g. Robichaud, Villard & Machtans 2002), some matrix types have been shown to be favourable to the movements of forest species, such as those created through agroforestry (Faria *et al.* 2006, 2007; Pardini *et al.* 2009) or low-intensity forestry (Barlow *et al.* 2007a, b; Fonseca *et al.* 2009). Maintaining functional connectivity is critical because it not only reduces Allee effects and maintains gene flow among subpopulations, but it may also sustain ecological processes such as pollination and seed dispersal (Levey *et al.* 2005; Damschen *et al.* 2006; Hadley & Betts 2012).

CONCLUSION

Understanding the interactive effects of habitat amount and configuration is a much more challenging issue than only considering habitat loss because nonlinear (threshold) and synergistic or antagonistic effects are generally present. However, these challenges can be viewed as an opportunity for innovation, given the flexibility that the management of habitat configuration and landscape composition offers to conservation planners. For example, we argued that in some circumstances, strategic addition of landscape elements may promote functional connectivity even though this will be interpreted through some metrics as an increase in fragmentation. Nonetheless, if the focus is on reachable habitat rather than on the number of habitat fragments, such interventions may increase population persistence (Saura & Rubio 2010). When conservation funds are limited or habitat restoration cannot be conducted over extensive areas, accurate prediction of the effects of habitat configuration and matrix composition on population viability and ecological services should be a research priority. Yet, surprisingly few large-scale experimental systems are being monitored to test strategies to manage habitat configuration and landscape composition in fragmented landscapes. Conservation researchers and practitioners must embrace this complex task to ensure that fragmentation effects are mitigated, especially in the context of rapid climate change.

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