



The fragmentation paradox: habitat amount and configuration as foci of conservation planning and research

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Review

1 **The fragmentation paradox: habitat amount and configuration as foci of**
2 **conservation planning and research**

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24 Summary

25 1. Research addressing the effects of habitat fragmentation on species,
26 assemblages, or ecosystems has been fraught with difficulties, from its
27 conceptual foundation to statistical analyses and interpretation. Yet, it is critical
28 to address such challenges as land use intensification rapidly alters ecosystems.

29 2. Many studies have concluded that effects of habitat loss exceed those of
30 fragmentation *per se*, even though there is also ample evidence from different
31 biomes and taxa that habitat edges, matrix structure/composition, or functional
32 connectivity influence species persistence.

33 3. To address this *fragmentation paradox*, we propose a conceptual model to
34 encourage conservation planners and researchers to identify portions of the
35 gradient in habitat loss where interaction effects between amount and
36 configuration are most likely to be found. Habitat configuration generally has a
37 low influence at both ends of the gradient, whereas species exhibit a narrow or
38 wide band at intermediate values of habitat amount where spatial arrangement
39 and the nature of adjoining matrix matter.

40 4. On the basis of empirical examples, we expect that species that are relatively
41 tolerant to fragmentation of their habitat will exhibit, along a gradient in habitat
42 amount, a wide band where amount and configuration interact, whereas
43 fragmentation-sensitive species will exhibit a narrow band above and below
44 which habitat configuration no longer matters.

45 5. *Synthesis and applications.* Stemming habitat loss should be a top priority for
46 conservation planners. Researchers should focus their attention on its indirect

47 effects on biodiversity through fragmentation sensu strictu, i.e. alteration of the
48 spatial arrangement of remnant habitat and matrix. This research should help
49 identify windows of opportunity where habitat configuration can mitigate to
50 some extent the effects of habitat loss through the maintenance of functional
51 connectivity.

52 **Key-words:** dispersal; edge effects; functional connectivity; land use
53 intensification; landscape matrix; movement ecology; spatial arrangement

54

55 **Introduction**

56 The long-standing debate regarding the relative influence of habitat loss versus
57 fragmentation seems to have arrived at a crossroads. Although the two
58 phenomena occur simultaneously in many circumstances and their effects are
59 often confounded (Smith et al. 2009), there are theoretical and practical reasons
60 to reconsider the relevance of this debate. From a theoretical perspective, there
61 is evidence for the effects of both phenomena on different taxa in various biomes
62 but we have largely failed to empirically identify ranges along the gradient of
63 habitat loss where habitat fragmentation matters. From a practical viewpoint, we
64 are condemned to succeed because land use intensification is changing the face
65 of the earth (Gibson et al. 2011; Lindenmayer, Cunningham & Young 2012) and
66 this is occurring at an increasing rate (Butchart et al. 2010). Although much has
67 been written on this theme, a reassessment is timely if we are to reconcile
68 conservation science and practice.

69 In this paper, we critically review the literature addressing the ecological
70 effects of landscape change and propose a framework to better orient
71 conservation research and policy. From a research perspective, we submit that
72 the role played by habitat loss in the biodiversity crisis is self-evident and that
73 research should focus on its non-trivial, indirect effects expressed through
74 habitat fragmentation and matrix influences. Stemming habitat loss remains a
75 top priority for conservation but the spatial pattern of habitat loss also matters
76 and research can provide major insight to optimize habitat conservation or
77 restoration strategies.

78 For the purposes of this paper, we refer to *fragmentation* as the process
79 through which a focal habitat type is “broken apart” (Fahrig 2003) by the
80 creation of land cover types generally unsuitable for reproduction and more or
81 less permeable to movements that are collectively referred to as the *matrix*. The
82 diverse spatial arrangements of focal habitat resulting from past habitat loss (e.g.
83 habitat fragment size, shape, and degree of aggregation or structural
84 connectivity) are referred to as *habitat configuration*. Finally, *landscape structure*
85 designates both habitat and matrix types present (*landscape composition*) and
86 their spatial arrangement (*landscape configuration*) (Fig. 1).

87 We call “fragmentation paradox” the considerable disparity observed
88 among studies in the relative influence of habitat fragmentation vs habitat loss as
89 leading causes of biodiversity loss. Although there is evidence for a prominent
90 role of habitat loss/amount over habitat fragmentation/configuration effects on
91 many biodiversity parameters (e.g. Fahrig 2003; Mortelliti et al. 2011; Smith,
92 Fahrig & Francis 2011), there is also ample evidence for both fragmentation and

93 matrix effects on functional connectivity, landscape permeability, and edge
94 structure/amount on species presence, abundance, or reproduction in many
95 biomes (reviewed by Ewers & Didham 2006).

96

97 **Challenges facing fragmentation research**

98 Disentangling the effects of habitat amount, configuration and matrix
99 composition on biota is especially challenging for at least five reasons: (1) most if
100 not all configuration metrics covary with habitat amount (Fahrig 2003 and
101 references therein), thus challenging the distinction of their independent effects;
102 (2) fragmentation effects may be restricted to the lower (Andrén 1994; Radford,
103 Bennett & Cheers 2005; Betts et al. 2006) or middle (Pardini et al. 2010,
104 Martensen et al. in press) portions of the gradient in habitat amount, further
105 complicating their detectability; (3) landscape units with similar habitat
106 amounts but varying configurations are uncommon in the real world, especially
107 for a given matrix type (e.g. Gobeil & Villard 2002; but see McGarigal & McComb
108 1995; Robichaud, Villard & Machtans 2002; Prist, Michalski & Metzger 2012); (4)
109 biological responses to changes in landscape structure are complex and not
110 always easy to detect because they may vary among species or functional groups
111 (Van Houtan et al. 2007; Vetter et al. 2011), geographic regions (Baldi 1996;
112 Lindell et al. 2007; Betts & Villard 2009), spatial extents (Deconchat, Brockerhoff
113 & Barbaro 2009; Smith, Fahrig & Francis 2011; Banks-Leite, Ewers & Metzger, in
114 press), or as a function of time since fragmentation took place (Petit & Burel
115 1998; Lindborg & Eriksson 2004; Callens et al. 2011).

116 Teasing apart effects of habitat loss and fragmentation can be challenging
117 and there is no consensus on the best statistical approaches to do so. On the
118 basis of simulations, Smith et al. (2009) recommended to estimate the
119 independent effects of habitat loss and fragmentation using standardized partial
120 regression coefficients obtained from multiple regression models. Variation
121 partitioning has also been used to separate the independent effects of those
122 factors on the structure of species assemblages (Legendre 2008; Banks-Leite,
123 Ewers & Metzger 2012). Didham, Kapos & Ewers (2012) have proposed to use
124 structural equations to model the independent and combined (interdependent)
125 effects of these parameters and to investigate direct and indirect pathways
126 through which landscape change affects biodiversity. Furthermore, these
127 authors argued that “effects of habitat loss are mediated in large part by
128 changing the spatial arrangement of habitat – that is, habitat loss acts via the
129 change in habitat arrangement, not *independently* of it” (Didham, Kapos & Ewers
130 2012: 163-164). Our goal here is not to enter a statistical debate, but rather to
131 propose a conceptual model assisting researchers interested in contrasting
132 species responses to gradients in landscape change.

133 Not surprisingly, the numerous attempts to detect consistent patterns in
134 the responses of different species, guilds, or functional groups to fragmentation
135 of their habitat (e.g. Debinski & Holt 2000; Henle et al. 2004; Lampila et al. 2005;
136 Vetter et al. 2011; Banks-Leite, Ewers & Metzger 2012) have tended to yield few
137 generalizations. Some authors have even concluded that a search for generalities
138 across species is probably not the best avenue and that holistic conservation
139 strategies over multiple scales are warranted (Banks-Leite, Ewers & Metzger, in
140 press).

141

142 **Habitat loss, habitat fragmentation, and ecological research**

143 *Habitat* being a species-specific concept, the occurrence and abundance of all
144 species should increase with *habitat amount*, as each fragment becomes more
145 accessible as habitat becomes connected (Boscolo et al. 2008, Awade et al. 2012)
146 and approaches the percolation threshold (King & With 2002). The pool of
147 immigrants would also be expected to increase with habitat amount (Venier &
148 Fahrig 1998; Betts & Villard 2009; Hadley & Betts 2012). Increasing habitat
149 amount may also mitigate some detrimental effects of the matrix or proximity to
150 edges. Hence, habitat amount per se, and steps to maintain or increase it, are
151 priorities for conservation planning but its indirect effects on functional
152 connectivity and matrix/edge effects still require in-depth scientific
153 investigation.

154 There is theoretical and empirical evidence from metapopulation models
155 (e.g. the incidence function; Hanski & Gilpin 1997) and other spatially explicit
156 models that different configurations of a given amount of habitat can affect
157 functional connectivity (Fig. 2) or species persistence (Fahrig 1997), at least over
158 certain portions of the gradient in habitat amount (Fig. 2) and thus, alter the
159 balance between local extinctions and recolonisations. Several authors have
160 suggested that habitat configuration is particularly significant below a certain
161 amount (called the “fragmentation threshold”), usually around 20-30% (Fahrig
162 1997, Betts, Forbes & Diamond 2007). In landscapes where habitat amount is
163 high enough to meet the requirements of species of conservation concern, but
164 insufficient to allow for extensive movement, research can (and should) make

critical contributions to identify priority interventions to maintain/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; Poulin & Villard 2011; Falk, Nol & Burke 2011) and permeability to the movements of certain taxa (Kennedy & Marra 2010; Villard & Haché 2012), and to identify drivers of habitat degradation and determine their relative influence (Laurence et al. 2002; Pérot & Villard 2009; Knowlton & Graham 2011). Thus, habitat amount is always an important consideration, but researchers should focus on portions of the gradient in habitat amount where habitat configuration potentially matters to reduce or mitigate 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, it may also result from minor habitat gain/loss. For example, in landscapes where habitat is sparse from the perspective of a given species, ecological restoration may significantly increase functional connectivity (and thus, decrease fragmentation) through the addition of small patches or linear elements (Fischer & Lindenmayer 2002; Lloyd & Marsden 2011). At the other end of the scope, when habitat amount and structural connectivity are high, roads may alter movements of certain species (Merriam et al. 1989; Mader, Schell & Kornacker 1990; Develey & Stouffer 2001; Dyer et al. 2001; Gravel,

189 Mazerolle & Villard 2012) and, in some cases, fragment their populations (Epps
190 et al. 2005; Proctor et al. 2005; Lesbarrères et al. 2006; Clark et al. 2010) despite
191 the fact that the total area disturbed is modest at a landscape scale. Thus,
192 focusing on the indirect effects of habitat loss by considering how landscape
193 configuration can influence functional connectivity in fragmented landscapes
194 may be especially insightful to optimize conservation actions. Indeed, different
195 options to add a given amount of habitat can have drastically different outcomes
196 for fragmentation-sensitive taxa (Fig. 2). Hence, it is important to identify cases
197 where habitat configuration is relatively independent of habitat amount, and
198 then predict configurations resulting in higher functional connectivity.

199

200 **A conceptual model to integrate habitat amount and configuration**

201 Data from real landscapes and from simulations in neutral landscapes indicate
202 that changes in habitat amount in very low (< 20%) or very high (>80%)
203 portions of the gradient correspond to a highly restricted range of variation in
204 fragmentation parameters (Fig. 3) compared to intermediate habitat amount
205 (Neel, McGarigal & Cushman 2004; Oliveira & Metzger 2006). Hence,
206 theoretically at least, habitat fragmentation per se is more likely to play a greater
207 role at intermediate values along the gradient in habitat amount.

208 Finding minimal or critical values of habitat amount is already a challenge
209 in itself, which has been systematically pursued using different theoretical
210 backgrounds such as the island biogeography theory (e.g. minimum habitat
211 requirements), population demography and genetics (e.g. area supporting a

212 “minimum viable population”), or metapopulation theory (e.g. “metapopulation
213 capacity”; Hanski & Ovaskainen 2002). However, if habitat amount is strongly
214 related to habitat configuration, it follows that minimum requirements of habitat
215 amount will be influenced by habitat configuration and that they will be higher
216 when configuration impedes movement (Fig. 4a). Hence, we hypothesize that
217 specific portions of a gradient in habitat amount will be characterized by the
218 interaction of habitat loss and fragmentation effects on species persistence,
219 whereas in other portions, only habitat loss will matter (Fig. 4a). Minimum
220 habitat requirements can be higher or lower according to species sensitivity to
221 habitat loss, thus influencing the specific location along the gradient where
222 regional extirpation will be expected (Fig. 4b). Furthermore, depending on life
223 history characteristics of species, the width of the interacting region will also
224 vary (Fig. 4b). Specifically, the relative tolerance of species to habitat
225 fragmentation may restrict or expand the range of habitat amount where it can
226 occur.

227 The literature is replete with examples of species’ sensitivity to habitat
228 loss. However, research is needed to better understand the relative tolerance of
229 different species to habitat fragmentation. According to our conceptual model, a
230 species with a high tolerance to fragmentation should be affected by
231 fragmentation over a wider range of habitat amount, persisting in landscapes
232 with favourable configurations when habitat amount is low (Fig. 4). The white-
233 shouldered fire-eye (*Pyriglena leucoptera* Vieillot) is a good example of this
234 situation. This understory bird species from the Brazilian Atlantic forest
235 occupies landscapes featuring a wide range of habitat amount (e.g. >10%) and

236 should at least be influenced by fragmentation in landscapes with 10-50%
237 habitat (Martensen et al. in press). At the lower end of this range, this species
238 occurs in landscapes whose fragments are either large enough to accommodate a
239 breeding pair, or close enough to allow functional connectivity (i.e. landscape
240 supplementation: Dunning, Danielson & Pulliam 1992; Villard, Merriam &
241 Maurer 1995; Martensen et al. 2008; Boscolo & Metzger 2011; Banks-Leite,
242 Ewers & Metzger 2012). In more forested landscapes, with up to 50% habitat,
243 the white-shouldered fire-eye can occupy smaller and more isolated patches, yet
244 it still responds to landscape configuration (Banks-Leite, Ewers & Metzger
245 2012). A similar pattern can be found in the Scarlet Tanager (*Piranga olivacea*
246 Gmelin), a Nearctic Neotropical migrant bird species that can occupy landscapes
247 representing a broad range of habitat amounts (>10%), but still respond to fine-
248 scale habitat configuration (Villard, Merriam & Maurer 1995; Villard, Trzcinski &
249 Merriam 1999; Hames et al. 2001) even in landscapes with >20% potential
250 habitat. Fraser & Stutchbury (2004) have shown that this species can move
251 frequently among small, spatially aggregated fragments.

252 Species with a low tolerance to fragmentation are expected to respond to
253 this phenomenon over a narrower range of habitat amount, and will generally
254 depend more strongly on local habitat quality or have a low ability to move
255 across the matrix, in spite of their large area requirements. For example, the
256 White-browed Foliage-gleaner (*Anabacerthia amaurotis* Temminck), a red-listed
257 understory bird species, breeds in pristine unbroken Atlantic forest but also
258 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, in press).

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 and Metzger 2006; Barlow et al. 2007; 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 can thus be a valuable alternative to maintain a species in landscapes where an increase in habitat amount is impossible over the short term (Fig. 5), e.g. in tropical areas where soils have been degraded following deforestation.

Thus far, research has shown that fragmentation effects on some species can be mitigated through the use of scattered trees or small patches acting as stepping stones for movements (Fischer & Lindenmayer 2002; van der Ree, Bennett & Gilmore 2004; Lloyd & Marsden 2011; Leidner & Haddad 2011). Linear landscape elements (“corridors”) may also enhance movements across relatively impermeable matrices (Tewksbury et al. 2002; Robichaud, Villard & Machtans 2002). Finally, matrix management may offer creative options for facilitating movement of organisms through different processes (emigration

282 from a home patch, immigration into a new habitat patch, and inter-patch
283 movements; Bowler & Benton 2005). Despite the challenge of quantifying matrix
284 permeability because it may vary spatially and temporally (e.g. Robichaud,
285 Villard & Machtans 2002), there are examples of matrix types favourable to the
286 movements of forest species, such as those created through agroforestry (Faria
287 et al. 2006, 2007, Pardini et al. 2009) or low-intensity forestry (Barlow et al.
288 2007a,b, Fonseca et al. 2009). Maintaining functional connectivity is critical
289 because it not only reduces Allee effects and maintains gene flow among
290 subpopulations, but it may also be critical to maintain ecological processes such
291 as pollination and seed dispersal (Levey et al. 2005; Damschen et al. 2006;
292 Hadley and Betts 2012).

293 Even though patch level effects are relevant to population viability, they
294 should not be a focus of habitat fragmentation research because one of the few
295 generalities emerging from the literature on landscape ecology is that no single
296 patch, even larger ones, can maintain its ecological integrity in isolation (Janzen
297 1983; Sodhi et al. 2010; Callens et al. 2011; Olds et al. 2011). Banks-Leite et al.
298 (in press) have shown that forest patch size had little influence on avian species
299 composition, the key predictor being forest amount at the landscape scale.

300

301 **Conclusion**

302 Understanding the interactive effects of habitat amount and configuration is a
303 much more challenging issue than only considering habitat loss because non-
304 linear (thresholds) 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 composition offers to conservation planners. 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 landscape configuration and 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 (Marini et al. 2009).

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587 **Figure legends**

588

589 **Fig. 1.** Schematic example of changes in landscape structure associated with loss
590 and fragmentation of a focal habitat type (in black), as well as shifts in matrix
591 composition (white and gray tones). Changes from landscapes a) to c) and b) to
592 d) pertain to *landscape composition*, without alteration of the *configuration*
593 (spatial arrangement) of the focal habitat. Changes from landscapes a) to b) and
594 c) to d) affect both *landscape configuration* and *composition*, resulting in a
595 modification of *landscape structure*. Changes in matrix composition may in turn
596 affect *landscape permeability* to movements of organisms.

597 **Fig. 2.** The spatial arrangement of habitat patches matters. Landscapes with the
598 same amount of habitat, and also with the same number of patches of the same
599 size, but in different spatial locations may result in situations where functional
600 connectivity is completely different. In (A), patches are too isolated and there are
601 no biological fluxes among them (similar to a “metapopulation in non-
602 equilibrium”) while in (B), the displacement of four patches allows free
603 movement among all patches (like in a “patchy metapopulation”). In situations
604 (C) and (D), the insertion of a small patch (in black) in different locations may
605 have very different effects on functional connectivity and the corresponding
606 habitat network.

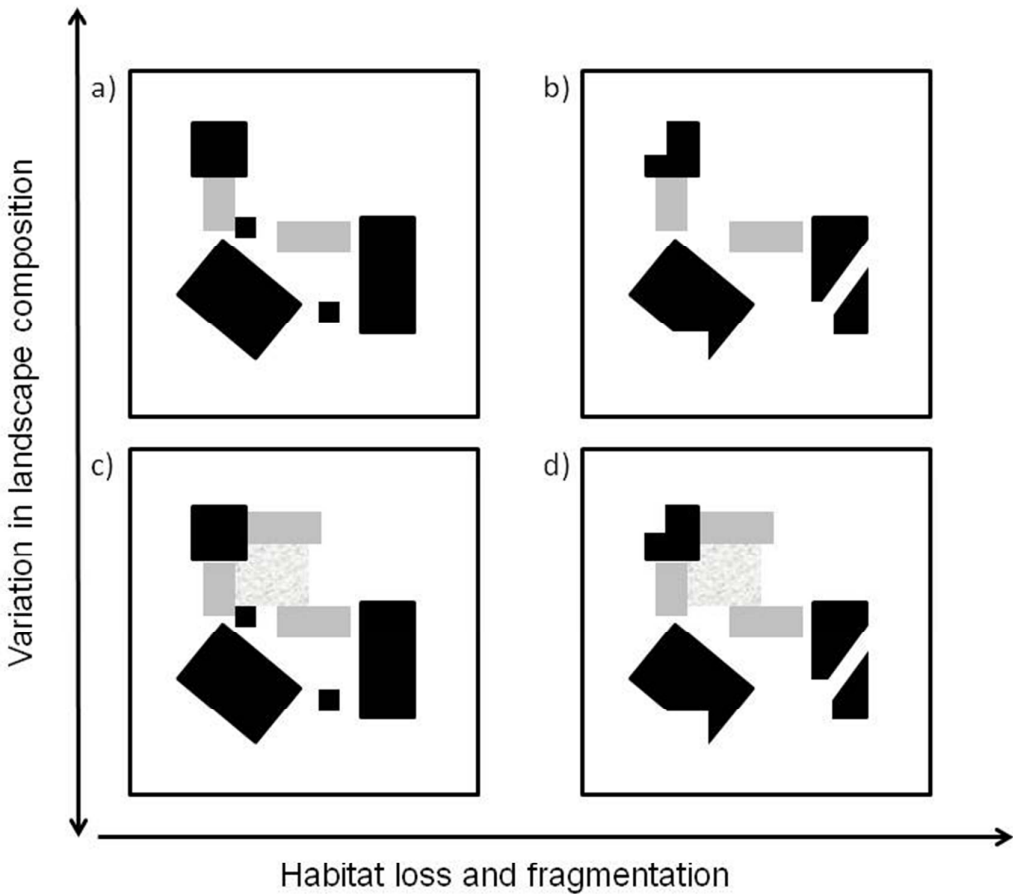
607 **Fig. 3.** Expected relationship between habitat amount and its fragmentation
608 (measured for example by the number of patches or the density of edges
609 between habitat and matrix) for landscapes with different degrees of
610 aggregation. At intermediate habitat amounts, landscapes are expected to show

611 higher variability in habitat fragmentation compared to landscapes with high or
612 low amounts of habitat.

613 **Fig. 4.** Theoretically, the minimum habitat amount required by each species
614 depends on some landscape characteristics, such the matrix composition and the
615 spatial arrangement of habitat, which can both affect habitat accessibility. When
616 landscape structure is more favourable, species can require less habitat in
617 comparison with less favourable landscapes. We can thus suppose that species
618 occurrence and abundance are regulated at the same time by habitat loss and
619 fragmentation at intermediate condition of habitat amount, while when habitat
620 is more abundant only habitat loss will act and when habitat is rare the species
621 will not survive (a). This general framework can help to distinguish species with
622 different tolerance to fragmentation and sensitivity to habitat loss (b).

623 **Fig. 5.** Examples of how habitat configuration and matrix composition may have
624 profound effects on functional connectivity. Considering a reference situation (A),
625 the creation of stepping stones (B), thin corridors (C) or the improvement of
626 matrix permeability (D) may all result in an increase in functional connectivity
627 among previously isolated habitat patches.

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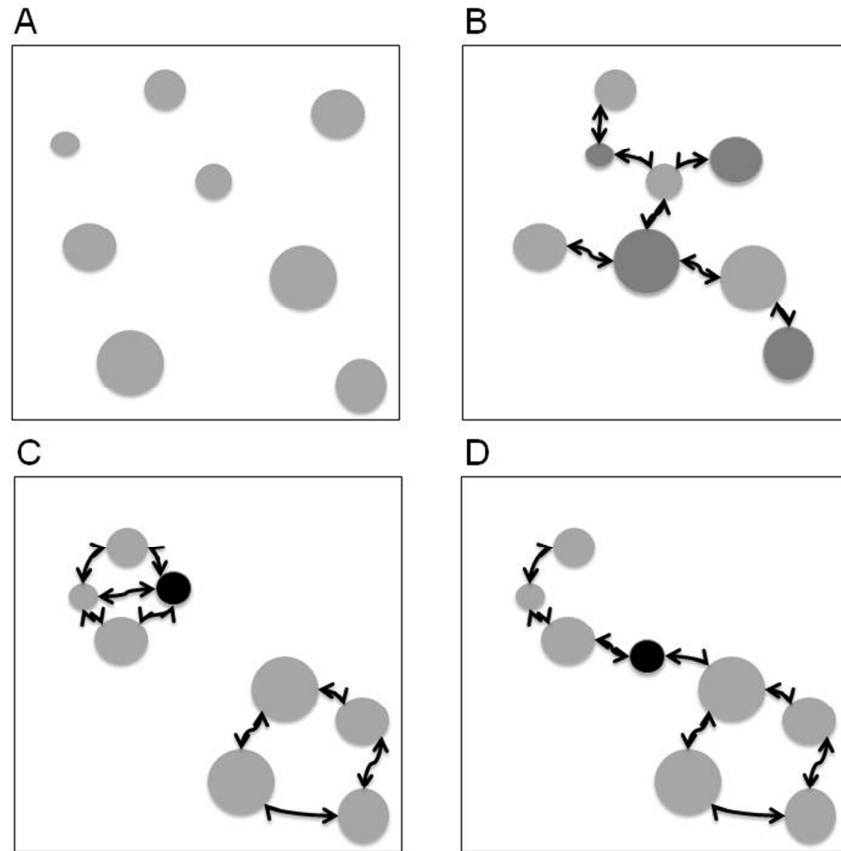
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633 Fig. 1



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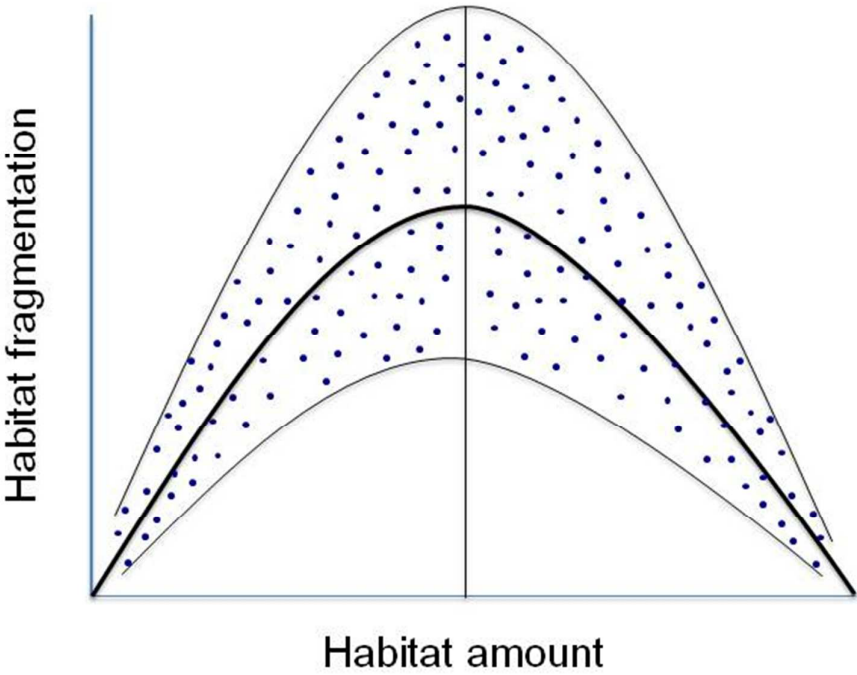
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639 Fig. 2

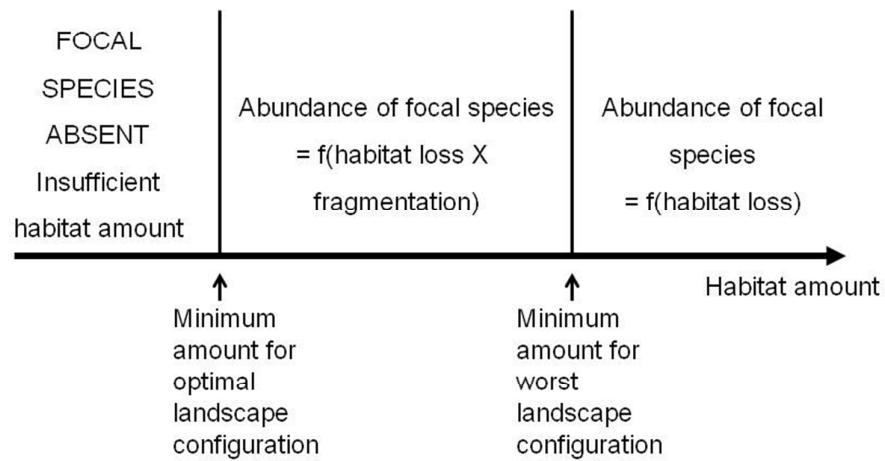


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Fig. 3

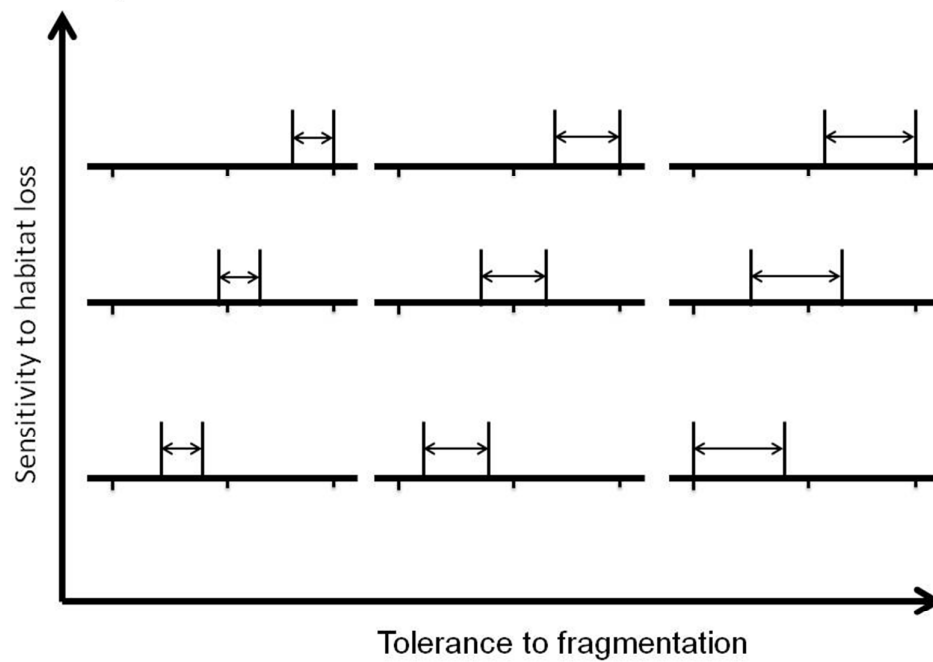
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a)



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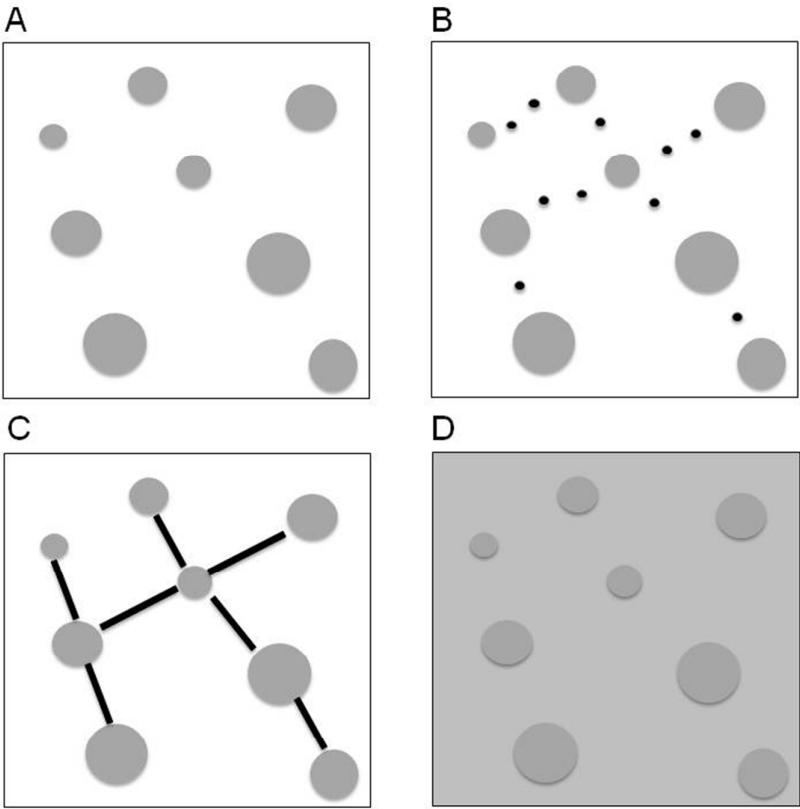
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649 Fig. 4



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655 Fig. 5