

Effect of landscape connectivity on plant communities a review of response patterns

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1 **Title:**

2 Effect of landscape connectivity on plant communities: a review of response patterns

3

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14 **Abstract:**

15 Context. Fragmentation in agricultural landscapes is considered as a major threat to
16 biodiversity. Thus, ecological corridors are deployed at multiple scales to increase connectivity.

17 However, there is limited consensus about their efficiency, especially for plants.

18 Objectives. We assimilated existing knowledge to assess whether and how landscape
19 connectivity impacts plant communities.

20 Methods. We reviewed published literature across more than 20 years, providing an overview
21 on the influence of connectivity on plant communities.

22 Results. We found that landscape connectivity has a varying and complex influence on the
23 composition and diversity of plant communities (*i.e.* community taxonomic structure), due to
24 the multiplicity of factors that modulate its effect. Our understanding of how of landscape
25 connectivity impacts the dispersal of plants is improved by using biological traits (*i.e.*
26 community functional structure). Finally, we showed that landscape connectivity promotes
27 actual dispersal between connected communities.

28 Conclusions. This review emphasises the pertinence of trait-based and actual dispersal
29 approaches to improve our understanding and ability to predict the effect of connectivity loss
30 on plant communities, allowing us to identify new prospects for future research.

31

32 **Keywords:** plant communities, traits, seed dispersal, actual dispersal, ecological corridors

33 **Introduction**

34 Anthropogenic activities, including urbanization and agricultural intensification, present major
35 threats to biodiversity, notably through their effects on landscape fragmentation (Stoate et al.
36 2001; Kato et al. 2009; Haddad et al. 2015). Landscape fragmentation impacts the populations
37 of plants through two distinct effects: habitat loss (*i.e.* a decrease in habitat area) and
38 connectivity loss (*i.e.* decreased plant dispersal among remnant patches; Taylor et al. 1993)
39 (Fahrig 2003; Fischer and Lindenmayer 2007). Because of their sessile way of life, plants are
40 particularly vulnerable to these effects, and many studies have reported a strong decline in
41 floristic diversity in fragmented agricultural landscapes (Andreasen et al. 1996; Kleijn and
42 Verbeek 2000; Luoto et al. 2003; Baessler and Klotz 2006; Kleijn et al. 2009). The effect of
43 habitat area on plant diversity is well established (*e.g.* Scanlan 1981; Dzwonko and Loster 1988;
44 Zacharias and Brandes 1990; Honnay et al. 1999; Godefroid and Koedam 2003; Gignac and
45 Dale 2007). Small patch size increases extinction risk by reducing carrying capacity.
46 Consequently, populations in smaller habitats are more susceptible to extinction, due to
47 demographic stochasticity (MacArthur and Wilson 1967). Only in the last two decades have
48 studies begun investigating how connectivity loss affects plant diversity and the corresponding
49 mechanisms; consequently, there is a low level of synthesis of existing knowledge.

50 Depending on the intensity of connectivity loss, the spatial distribution of species might
51 range from a continuous population to a set of isolated populations with a metapopulation
52 structure (*i.e.* a network of local populations linked by dispersal fluxes, Hanski 1994) as an
53 intermediate case. More recently, the metapopulation concept has been extended to the
54 community level (*i.e.* metacommunity concept, Leibold et al. 2004). A metacommunity refers
55 to a set of local communities that are linked by the dispersal of multiple potentially interacting
56 species (Wilson 1992). The strong interest in metacommunity theory has given rise to four
57 paradigms to describe metacommunities: i) species sorting (*i.e.* habitat patches are

58 environmentally heterogeneous with high enough dispersal to enable species to fill niches
59 within habitat patches because of niche diversification); ii) mass effects (*i.e.* habitat patches are
60 environmentally heterogeneous and high dispersal enough override local dynamics); (iii) patch
61 dynamics (*i.e.* habitat patches are environmentally homogeneous and species differ in their
62 ability to disperse. Along a colonisation–competition trade-off, successful colonisers
63 outcompete poor competitors and *vice versa*); and iv) neutral models (*i.e.* species do not differ
64 in their fitness or niche) in the case of ecological drift (Leibold et al. 2004; Logue et al. 2011).
65 These models formulate different hypotheses on the relative importance of dispersal, habitat
66 heterogeneity and interactions between species in the structuring mechanisms of local
67 communities (Leibold et al. 2004; Logue et al. 2011). Plant disperse passively between habitat
68 patches via pollen and/or seeds. However, this process is only successful if habitat patches are
69 sufficiently connected (Fahrig and Merriam 1985; Bowne and Bowers 2004); in other words,
70 plant dispersal among source patches must be facilitated by suitable landscape elements (Taylor
71 et al. 1993). Landscape connectivity might be promoted by the occurrence of corridors between
72 favourable patches, such as continuous, relatively narrow, habitat bands connecting two patches
73 (Burel and Baudry 1999). However, connectivity might also include nonlinear or discontinuous
74 landscape features that are permeable to plant dispersal (Beier and Noss 1998; Chetkiewicz et
75 al. 2006). Thus, high connectivity between habitat patches might reduce the adverse effects of
76 fragmentation by facilitating genetic fluxes among local populations through plant dispersal
77 (Wilson and Willis 1975), which contrasts with animals for which all movements is concerned.

78 However, the ability of plants to disperse in fragmented landscapes might depend on
79 their dispersal strategy, with some being more or less able to promote frequent long-distance
80 dispersal events. For instance, if wind-dispersal or water-dispersal is generally achieved over a
81 long distance, depending on the intensity of the wind or current and the adaptations of the seeds,
82 gravity-dispersed plants (*i.e.* barochory) are dispersed more locally (Nathan et al. 2002;

83 Tackenberg 2003; Vittoz and Engler 2007; Pollux et al. 2009; Nilsson et al. 2010). Animal-
84 dispersed plants are dispersed over short distances of <100 m (*e.g.* by small animals, such as
85 insects, small mammals and some bird species) to long distances of several kilometres (*e.g.* by
86 large or migratory animals; Vittoz and Engler 2007). These vectors might be influenced
87 differently by landscape elements and, in turn, might influence plant responses to connectivity
88 loss. Within a certain type of dispersal mode, plant species might represent a large range of
89 capacities to disperse with respect to quantity (*i.e.* number of potential dispersers) and distance
90 (*i.e.* dispersal range) (Johst et al. 2002; Nathan 2006; Auffret et al. 2017), which might decrease
91 or increase their chance to disperse. These responses involve a selection of particular biological
92 traits (*i.e.* morphological, biochemical, physiological, structural, phenological or behavioural
93 characteristics of organisms that influence performance or fitness, Violle et al. 2007). At the
94 plant community scale, analyses of how these traits respond to connectivity might help us to
95 understand the processes that are involved, which would facilitate a more mechanistic analysis
96 of plant assembly in fragmented landscapes.

97 Because plants are sessile, the effect of connectivity on plant assemblages might be
98 time-dependent, with responses reflecting a relaxation time (*i.e.* the time taken for a community
99 of species to reach a new equilibrium after an environmental disturbance, Diamond 1972;
100 Kuussaari et al. 2009). By extension, the response of plant to connectivity might also reflect an
101 extinction debt, which is defined as the number or proportion of extant species predicted to
102 become extinct as the species community reaches a new equilibrium after an environmental
103 disturbance (Tilman et al. 1994; Ovaskainen and Hanski 2002; Kuussaari et al. 2009). The
104 response of plant assemblages to connectivity might also reflect an immigration lag, *i.e.* the
105 time that has elapsed between an immigration-committing forcing event (*e.g.* increasing
106 connectivity) and the establishment of an immigrating species (Jackson and Sax 2010). By
107 extension, this phenomenon would lead to immigration credit (Jackson and Sax 2010), which

108 is defined as the number of species committed to eventual immigration following a forcing
109 event (Kuussaari et al. 2009). In addition, temporal lags in extinction and immigration are
110 mediated by variation in traits across species under experimental situations (Haddad et al.
111 2015). Thus, considering the role of historical connectivity on the composition and diversity of
112 plant communities and how traits mediate the delayed response of plant might improve our
113 understanding of how plant species respond to connectivity loss.

114 Metacommunity theory recognizes that established local communities may additionally
115 be driven by stochasticity (which is eventually spatially correlated), local patch conditions and
116 species traits (*i.e.* colonisation vs. competition trade-offs) (Mouquet and Loreau 2003). As a
117 result, recent studies argued that assessing how connectivity affects established communities in
118 habitat patches is subject to bias. Indeed, once a propagule arrives in a patch, its ability to
119 establish depends on a large range of local factors linked to local habitat quality (*e.g.*
120 management, land-use history, Brudvig 2016) and biotic interactions (*e.g.* plant-plant, plant-
121 animal, plant-soil interactions, Archer and Pyke 1991; Pyke and Archer 1991; Fukami and
122 Nakajima 2013). Therefore, it might be difficult to disentangle the effects of landscape
123 connectivity and local filters. In addition, the increase of connectivity might indirectly affect
124 the establishment and coexistence of plants in the community by promoting the displacement
125 of: i) organisms that might predate on (*e.g.* herbivores and granivorous species, Orrock et al.
126 2003; Orrock and Damschen 2005; Rossetti et al. 2017) or parasitize seeds (*e.g.* Sullivan et al.
127 2011), or ii) strong competitors that once, they arrived in a local patch, drive local biotic
128 interactions and outcompete less competitive species (Simberloff and Cox 1987; Mouquet and
129 Loreau 2003, *e.g.* exotic invasive plant species, Minor et al. 2009; Minor and Gardner 2011).
130 To assess the direct effect of connectivity on seed dispersal, Calabrese and Fagan (2004)
131 proposed the concept of actual functional connectivity (Fig. 1 and Box 1). This concept is based
132 on the direct assessment of seed fluxes depending on habitat connectivity. This form of direct

133 assessment might reflect the effect of connectivity on the process of dispersal alone,
134 independent of other local factors that are difficult to standardise.

135 The number of studies analysing the influence of landscape connectivity on biodiversity
136 has increased considerably since the early part of the 21st century (Ayram et al. 2016). To
137 facilitate the identification of general patterns, reviews have been compiled on how connectivity
138 affects global biodiversity (Murphy and Lovett-Doust 2004; Haddad and Tewksbury 2006;
139 Gilbert-Norton et al. 2010; Haddad et al. 2011, 2015; Fletcher et al. 2016). These reviews have
140 provided evidences of the effect of connectivity at different levels of organization (individuals,
141 populations and communities) essentially through experimental approaches (Haddad and
142 Tewksbury 2006; Haddad et al. 2011, 2015) or sometimes coupled with correlatives ones
143 (Murphy and Lovett-Doust 2004; Gilbert-Norton et al. 2010; Fletcher et al. 2016). However,
144 these reviews mostly focus on animal biodiversity. When these reviews consider existing
145 literature on plants, the response of plants to connectivity is usually often assessed at the
146 population level and under experimental conditions and does not take into account the traits of
147 plant species (Murphy and Lovett-Doust 2004; Gilbert-Norton et al. 2010; Haddad et al. 2011,
148 2015; Fletcher et al. 2016). As a result, our understanding of the role of connectivity for plants
149 remains limited, especially at the community level. The effect of connectivity on plant
150 communities cannot be predicted from its effect on plant populations and individuals, as
151 communities incorporate distinct properties linked to their dynamics such as priority effects
152 (Fukami 2015) and successional changes in species diversity over time. This lack of knowledge
153 may be particularly problematic for the conservation of plant biodiversity, which aims to go
154 beyond single-species approaches (Groves et al. 2002).

155 In the present review, we aimed to provide a synthesis of existing scientific knowledge
156 on how connectivity loss influences plant communities. To achieve this synthesis, we only
157 considered studies that assessed connectivity and plant species responses at the community

158 level. Connectivity was analysed under experimental approaches through the presence or
159 absence of an experimentally-created corridor between patches (Fig. 1 and Box 1) or under
160 correlative approaches using quantitative indices. Quantitative connectivity assessments were
161 based on isolation metrics such as Euclidean distance, structural connectivity indices (see
162 various examples in the main text), least-cost distance and resistance distance (respectively
163 derived from graph and circuit theory, potential functional connectivity) (Fig. 1 and Box 1).
164 This approach included: i) analysis of individual species responses across most species of the
165 community and, ii) aggregated measures across most species of a given community (for more
166 details, see Appendix S1).

167 Specifically, we present how landscape connectivity influences the richness and
168 composition of plant communities (section 1). We also review how plants respond to
169 connectivity from a mechanistic perspective (related to dispersal vector mode and plant
170 dispersal traits), to demonstrate that traits may help to define species sensitivity to connectivity
171 loss (section 2). We also evaluate how time affects plant taxonomic and functional response to
172 connectivity (section 3). Finally, we review how connectivity drives actual dispersal (section
173 4). We conclude that landscape connectivity influences plant communities as a filter for species
174 and traits. We also emphasize that trait-based and actual dispersal approaches are the most
175 relevant for predicting how connectivity loss affects plant communities. We use our findings to
176 suggest further research needs.

177

178 **Contrasted effect of landscape connectivity on plant community taxonomic structure**

179 Higher connectivity facilitates plant dispersal and thus decreases the probability of local
180 extinction. Thus, high connectivity might influence the taxonomic structure of communities
181 (*i.e.* the composition and diversity of plant communities), increasing species diversity and
182 similarity in composition between connected patches.

183

184 *Plant community diversity*

185 How connectivity affects species diversity has been a central question in landscape ecology
186 over the last two decades. Early studies tested this question by comparing pairs of patches that
187 were (or not) connected through a corridor. The effect of the presence/absence of a corridor on
188 plant diversity has been, for instance, addressed through the experimental manipulation of
189 connectivity between habitat patches. One of the most well-known designs is based at Savannah
190 River Site (South Carolina, USA), which supports a range of landscape designs embedded in a
191 forest matrix. In this experimental design, each landscape is composed of a central patch that is
192 connected to one peripheral patch by a corridor, and a peripheral patch that is not connected to
193 the central patch (Box 2). In this design, patches connected by a corridor displayed a richness
194 higher than 20% compared to the non-connected patches (Damschen et al. 2006). Plant species
195 richness also increases from 10 to 18% in the matrix surrounding the connected patches by a
196 mass spatial effect (Brudvig et al. 2009); thus, the presence of corridors might positively impact
197 adjacent landscape elements.

198 Another set of studies used connectivity measurements based on the Euclidean distance
199 or on the permeability of the landscape elements to dispersal. In the latter case, these
200 measurements incorporate the physical attributes of the landscape with or without information
201 about the organism of interest (structural or potential functional connectivity) and assess the
202 degree of connectivity for each habitat patch (Fig. 1 and Box 1). Depending on the ecosystem
203 type, landscape connectivity has a contrasting effect on community diversity. For instance, local
204 heathland species richness increases with structural connectivity [measured through the
205 Incidence Function Model index (IFM index) based on the area and the Euclidean distance to
206 other patches of similar habitat type, Hanski 1994; Moilanen and Nieminen 2002)] (Piessens et
207 al. 2004), whereas structural connectivity does not influence the richness and the density of

208 species (*i.e.* average number of species per square meter) of local plant communities in semi-
209 natural grasslands (Lindborg and Eriksson 2004; Helm et al. 2006; Cousins et al. 2007).
210 Lindborg and Eriksson (2004) demonstrated that this absence of a relationship with
211 connectivity was maintained at different spatial scales (1 km or 2 km radius). Only one study
212 demonstrated a negative influence of connectivity on local plant community richness in riverine
213 wetlands. Specifically, Bornette et al. (1998) reported that high connectivity decreases species
214 richness when assessing structural surficial connectivity between cut-off channels and the river
215 by quantifying the overflows and backflows of rivers into cut-off channels. Under these
216 conditions, high connectivity impedes recruitment due to over-frequent flood scouring or due
217 to nutrient-rich and turbid surficial waters being supplied to the wetland, which reduces species
218 richness.

219 Most studies investigating how landscape connectivity affects plant species
220 communities measure species richness at the alpha-scale (*i.e.* local diversity) (Bennett et al.
221 2006). In comparison, studies carried out at a gamma-scale (*i.e.* landscape diversity) remain
222 limited. For instance, Favre-Bac et al. (2014) reported that the structural connectivity of ditch
223 networks (*i.e.* number of disconnected network units) decreases species richness of ditch bank
224 communities when analysing 27 square sites of 500 x 500 m. This result might be attributed to
225 the influence of landscape heterogeneity, which might mitigate the negative effects of habitat
226 fragmentation (Tschardt et al. 2012).

227 Overall, no general pattern has been detected on the positive effect of corridors on plant
228 diversity through correlative approaches, contrary to experimental approaches (Haddad et al.
229 2015). Two possible explanations why correlative studies have failed to demonstrate a general
230 pattern are: i) the too low suitability and number of available habitat patches for plants to
231 colonise and establish, and ii) the lack of consideration of the quality (*e.g.* management
232 practice) of the landscape elements. These studies assessed connectivity through the presence

233 and identity of landscape elements to determine their permeability to dispersal, overlooking the
234 potential effect of the quality of these elements on their permeability.

235

236 *Plant community composition*

237 In fragmented landscapes, remnant habitat patches might be highly heterogeneous, causing
238 strong divergence in the composition of local communities (Tscharntke et al. 2012). In addition,
239 the amount of dispersal between remnant patches might strongly impact these dynamics
240 (Mouquet and Loreau 2003; Mouquet et al. 2006). When isolated, seed limitation is expected
241 to enhance divergence between local communities at the metacommunity scale, further
242 reducing their similarity (Mouquet and Loreau 2003; Tscharntke et al. 2012). A particular case
243 of dissimilarity in species composition, the nested subset (*i.e.* a community in which the species
244 present at species-poor sites constitute subsets of those from species-rich sites, Patterson and
245 Atmar 1986) was highlighted in heathland communities by Piessens et al. (2004). In these
246 systems, dissimilarity increases as structural connectivity decreases. The higher the landscape
247 structural connectivity, the higher the similarity of the community. Similar results were also
248 reported for communities of linear landscape elements, such as field margins, road verges and
249 ditches (Thiele et al. 2017). For instance, Thiele et al. (2017) tested three types of connectivity
250 metrics (Euclidian distance, potential functional connectivity: least-cost distance and resistance
251 distance, see Fig. 1 and Box 1.), and demonstrated that the results were independent of the way
252 that connectivity was evaluated.

253 Within local communities, fragmentation theoretically decreases species richness
254 because it acts as a strong ecological filter, selecting for species that are able to disperse and
255 survive in isolated patches. Thus, Haddad and Tewksbury (2006) theorised that specialist
256 species should be more affected by connectivity loss than generalist species, because the latter
257 group might perceive corridors as being of lower quality compared to the surrounding habitats.

258 Isolated patches might contain more generalist than specialist species in plant communities
259 compared to connected patches. In grassland communities, specialist species decrease to a
260 greater extent compared to generalist species in response to the loss of structural connectivity
261 (Adriaens et al. 2006; Brückmann et al. 2010; Evju et al. 2015). Adriaens et al. (2006) reported
262 that only specialist species are impacted by a change to the structural connectivity (assessed
263 with the IFM index) of grasslands, with the mean number of species per site decreasing by
264 about 37%. Similar results were obtained by Brückmann et al. (2010) and Evju et al. (2015).
265 For instance, Brückmann et al. (2010) recorded a decrease of 24-37% in the richness of
266 specialist species in grasslands in response to a total loss of structural connectivity (IFM index),
267 whereas generalists were not affected. Therefore, the effect of connectivity on plant species
268 depends on the degree of specialisation. Thus, different types of ecological corridors might
269 interact in a landscape. For instance, grassland corridors between forest patches might reinforce
270 the effect of forest corridors in connected forest patches only when considering generalist
271 species in forests. These interactions between corridor types might rank from potential
272 complementarity for generalist species to potential antagonism for specialist species, in which
273 one ecological corridor type is favourable while the other constitutes a barrier. Thus, it is
274 important to consider how complementary between the different types of ecological corridors
275 are in studies linking connectivity to plant communities. This consideration could be coupled
276 with the improved modelling of ecological corridor types through the use of SDMs (Species
277 Distribution Models; Guisan and Thuiller 2005), which represent a promising approach to
278 assess the permeability of landscape features to dispersal (*e.g.* Morato et al. 2014), rather than
279 expert knowledge (Rayfield et al. 2010; Spear et al. 2010; Zeller et al. 2012; Koen et al. 2012).
280
281 **Effect of landscape connectivity on the functional structure of plant communities**

282 Because of the contrasting results provided by taxonomic approaches, there is a growing need
283 to predict how plant communities respond to changes in connectivity. Analyses based on the
284 functional structure of communities (*i.e.* the composition and diversity of traits) might help to
285 improve our understanding of species responses by providing a mechanistic explanation (for a
286 detailed synthesis of these studies, see Table 1).

287

288 *Dispersal vector mode*

289 Studies using trait-based approaches initially focused on how plant dispersal vectors influence
290 their responses to connectivity. Plant dispersal vectors determine plant dispersal distance. For
291 instance, dispersal is close to the parent plant for gravity-dispersed species, and up to several
292 hundred metres or even kilometres for animal-, wind- and water- dispersed species (Sorensen
293 1986; Nathan et al. 2002; Tackenberg 2003; Vittoz and Engler 2007; Pollux et al. 2009; Nilsson
294 et al. 2010).

295 Animal-dispersal is oriented, and depends on animal behaviour and movement in the
296 landscape. There is broad consensus that animal movement is facilitated by landscape
297 connectivity (Murphy and Lovett-Doust 2004; Haddad and Tewksbury 2006; Gilbert-Norton et
298 al. 2010; Haddad et al. 2011, 2015; Fletcher et al. 2016); thus, animal-dispersed plant species
299 might be largely dependent on landscape connectivity. It is more difficult to predict how
300 connectivity affects wind-dispersed plants, as this type of dispersal is made at random or occurs
301 in relation to the dominant wind direction. Differences in these two plant dispersal vectors
302 might lead to different responses to connectivity. Damschen et al. (2008) surveyed the species
303 richness of bird-dispersed and wind-dispersed species over a seven-year period in the Savannah
304 River Site (Box 2). The authors demonstrated that, for both functional groups, the richness of
305 communities was lower in unconnected versus connected patches. However, this difference in
306 richness reached an asymptote for bird-dispersed species after five years, but not for wind-

307 dispersed species. This asymptote is due to the behaviour of birds that regularly visit all patches
308 of the experimental design. As a result, even isolated patches occasionally receive new
309 colonists, reducing the difference in species richness between connected and unconnected
310 patches over time. By contrast, the presence of an open corridor affects wind dynamics by
311 redirecting and promoting airflow and “ejection hotspots” (*i.e.* locations in which seeds have a
312 relatively high probability of being uplifted) in connected patches. These processes increase the
313 likelihood of seed uplift, and, therefore, the likelihood of seed redirection and bellow among
314 connected patches (Damschen et al. 2014). As a result, the difference in species richness
315 between connected and unconnected patches continues to increase over time. Based on the same
316 design, Brudvig et al. (2009) showed that the richness of animal-dispersed species increased by
317 13–19% per 100 m² in the surrounding matrix in response to connectivity, whereas no mass
318 spatial effect was found for wind-dispersed species. This result was due to a barrier effect of
319 the surrounding matrix of dense pine plantations on wind-dispersed species (Damschen et al.
320 2014). In contrast, animals were not restricted to the experimental design, moving in and out of
321 patches to the matrix, resulting in their contributing to the dispersal of plants. When assessed
322 in more correlative approaches, no particular influence of landscape connectivity (Euclidean
323 distance, structural and potential functional connectivity) was demonstrated on animal-
324 (external, internal and by ants) and wind-dispersed species (Piessens et al. 2005; Lindborg
325 2007; Evju et al. 2015; Thiele et al. 2017, but see contrasting results provided by Verheyen et
326 al. (2004) who only considered vertebrate-animal dispersal and wind dispersal), despite their
327 potential for long-distance dispersal. This finding suggests that, in real systems, the effect of
328 connectivity on the functional structure of plant communities is overshadowed by other
329 characteristics of the landscape, such as patch shape, which influences the quantity of the
330 interface with other habitats (*e.g.* Arellano-Rivas et al. 2016) or the fine-scale structuring of

331 corridors. In turn, this phenomenon influences the degree of permeability for animal- (*e.g.*
332 animal vector behavioural changes) and wind- (*e.g.* wind dynamics changes) dispersed species.

333 Another dispersal mode contributing to long-distance dispersal is hydrochory. Many
334 studies have investigated the role of water dispersal in structuring plant communities, in both
335 flowing and stagnant systems (for a review, see Nilsson et al. 2010). However, very few studies
336 present the effect of connectivity on water-dispersed plant communities. Favre-Bac et al. (2014)
337 showed that the richness of water-dispersed species at the landscape scale was independent of
338 ditch network connectivity, regardless of the measures of connectivity considered (*i.e.* total
339 ditch length, number of culverts, number of intersections and number of disconnected ditch
340 network subunits). However, similarity within local water-dispersed communities decreased
341 with the number of intersections, suggesting that these intersections act as barriers to dispersal
342 and cause a decrease of seed fluxes between communities (Favre-Bac et al. 2014). Similar
343 results were obtained by Piessens et al. (2005).

344 Other modes have been less studied, mostly because they were supposed to contribute
345 less to long-distance dispersal and, therefore, to plant sensitivity to connectivity. Nonetheless,
346 several studies have demonstrated a positive response of unassisted species (*i.e.* species without
347 dispersal structures, mostly gravity-dispersed species) in response to connectivity by both
348 experimental (Damschen et al. 2008) and correlative (Kolb and Diekmann 2005; Thiele et al.
349 2017) approaches. Damschen et al. (2008) demonstrated that the difference in unassisted
350 species richness between connected and non-connected patches was been six-fold greater after
351 seven years. A similar response was obtained by Thiele et al. (2017). The authors obtained a
352 positive relationship between connectivity (Euclidean distance and potential functional
353 connectivity) and similarity for unassisted species communities of linear landscape elements
354 (field margins, ditches, road verges). Despite the increase in unassisted species richness
355 (Damschen et al. 2008), the relative proportion of these species does not seem to be influenced

356 by connectivity within communities. When using a correlative approach, Lindborg (2007)
357 reported that the proportion of unassisted species in semi-natural grasslands was independent
358 of structural connectivity (IFM index). These results corroborate the work of Piessens et al.
359 (2005), who demonstrated that unassisted species are not sensitive to structural connectivity.
360 However, the dispersal mechanisms explaining the differential responses of unassisted species
361 in terms of richness and relative proportion to landscape connectivity have yet to be clarified.
362 As suggested by Damschen et al. (2008), these results challenge the notion that unassisted
363 species are truly unassisted in their dispersal, corroborating evidence from other studies
364 (Vellend et al. 2003; Higgins et al. 2003).

365

366 *Plant dispersal traits*

367 Beyond the dispersal mode, precise combinations of traits might favour the ability of plants to
368 produce a large number of potential dispersers (*e.g.* seed number, vegetative fragmentation),
369 and to be dispersed over long distances (*e.g.* seed mass, low terminal velocity, high gut
370 retention), with both characteristics corresponding to the definition of species dispersal ability
371 (Johst et al. 2002; Nathan 2006; Auffret et al. 2017). Thus, species with traits promoting high
372 dispersal ability might be less sensitive to connectivity loss.

373

374 Emergent groups to connectivity

375 Initially, studies that analysed the dispersal traits of plants in response to connectivity were
376 based on a functional group approach similar to the one proposed by Lavorel et al. (1997);
377 namely, emergent groups are groups of species that reflect natural correlation of biological
378 attributes. By coupling changes to plant occurrence or abundance along the gradient of
379 connectivity and trait-data on plant species, these studies analysed the syndrome of traits that
380 characterise plant sensitivity or resistance to connectivity.

381 One of the very first studies on emergent groups focused on forest communities (Kolb
382 and Diekmann 2005). These authors analysed species biological traits for two groups of plants:
383 one corresponding to sensitive plants (*i.e.* the occurrence of which decreases with structural
384 connectivity loss, evaluated through IFM index) and one corresponding to resistant plants (*i.e.*
385 the occurrence of which is not impacted by structural connectivity loss). Sensitive plants were
386 characterised by high clonality, few and heavy seeds and unassisted dispersal. Resistant plants
387 displayed assisted dispersal, no or little clonal growth and produced many and thin seeds. Traits
388 promoting local establishment instead of long-distance dispersal contributed to plant sensitivity
389 to connectivity loss. Using a similar approach, Adriaens et al. (2006) classified specialist
390 species from calcareous grasslands, using 16 life-history traits, and detected four different
391 groups. Higher structural landscape connectivity increased species richness in only one of the
392 groups, whereas the other groups were not affected. This group contains species that are
393 characterised by a perennial rosette with no vegetative multiplication and no long-distance
394 dispersal mode (*i.e.* ballistochory, ant-dispersed seeds, barochory). Such species are more
395 sensitive to connectivity loss, as they are less likely to recolonise and establish in patches after
396 extinction. The three other groups were not impacted by connectivity loss. These groups
397 included orchids (characterised by short flowering, low mass seeds and wind-dispersal), half-
398 rosette species (with fruity dispersules and seeds, with optional vegetative reproduction
399 mechanisms) and annual species (early and long flowering small autogamous annuals, low mass
400 and no long-distance dispersal mode). However, the use of a large set of many traits, including
401 ecological traits (*i.e.* linked with species niche), makes it difficult to disentangle the effect of
402 dispersal traits from the other traits when evaluating how species respond to connectivity loss.
403
404 Response traits to connectivity

405 Studies over the last two decades have focused on traits considered individually to define
406 individual response traits (*i.e.* traits reflecting the response of organisms to a given
407 environmental factor, Lavorel et al. 1997) to landscape connectivity. This approach differs from
408 the emergent group approach by analysing one trait at a time to characterise species sensitivity
409 to connectivity. Species that displayed similar trait values in response to connectivity are
410 designed as response groups of plants (*i.e.* group of species that respond in similar ways to a
411 given environmental factor for a given trait, Lavorel et al. 1997).

412 Verheyen et al. (2004) characterised species sensitivity for 17 species of temperate
413 forest communities to connectivity loss through the regression coefficient derived from the
414 regression model, using patch occupancy as the dependent variable and structural connectivity
415 (modified version of IFM index that incorporates patch age, Verheyen et al. 2004) as the
416 independent variable. Species characterised by lower numbers of seeds (and thus, a low number
417 of potential dispersers) were sensitive to connectivity loss. In ruderal (brownfields)
418 communities, Schleicher et al. (2011) demonstrated that wind-dispersed species sensitive to
419 structural connectivity loss are those characterised by lower seed number and higher terminal
420 velocity (*i.e.* rate at which a seed can fall in still air). High terminal velocity corresponds to
421 short dispersal range by reducing the probability of dispersal by air uplift, while reduced seed
422 number corresponds to a low number of potential dispersers. Consequently, both trait
423 expressions are indicative of low dispersal ability. Sensitive and resistant plants were the most
424 differentiated using a quotient of the seed number divided by terminal velocity. Moreover, the
425 authors found that the clearest differentiation between the two connectivity response groups
426 was obtained when combining seed number and terminal velocity in a quotient. These results
427 highlight a compensatory relationship between these two traits; high dispersal distance might
428 counterbalance low numbers of dispersers and *vice versa*. Favre-Bac et al. (2017a) used traits
429 directly linked to water-dispersal to analyse how ditch communities respond to connectivity

430 loss. The authors demonstrated that water-dispersed species that are highly sensitive to
431 structural connectivity loss are characterised by short and round seeds with low mass and low
432 buoyancy (Favre-Bac et al. 2017a). Low buoyancy does not favour long-distance dispersal in
433 low current systems because species do not tolerate long or frequent retention events when
434 being dispersed. The authors also demonstrated the role of seed form on the probability of being
435 retained by obstacles in stagnant ditches during dispersal events. In this case, long and thin
436 seeds might be better aligned to flow direction, and succeed better in passing obstacles, such as
437 culverts and intersections (De Ryck et al. 2012). This type of study advanced our understanding
438 of the factors that induce dispersal in the studied system, providing some predictions on the
439 mechanisms causing species resistance in less connected networks.

440 Some studies demonstrated that connectivity responses are associated to traits linked
441 with the ability of plants to establish in habitat patches. For instance, Favre-Bac et al. (2017a)
442 reported that, in highly branched ditch networks (*i.e.* where intersections constitute obstacles to
443 dispersal), the most resistant plants had higher seed germination rates. This higher seed
444 germination rate increased their ability to develop when blocked by obstacles during dispersal.
445 Other traits linked to further steps of plant growth, such as competition (for instance, plant
446 height) and duration of growth (life-cycle duration), were also investigated. It was found that
447 species with lower competition capacity and short life-cycles (in temperate forest communities,
448 Verheyen et al. 2004, in heathland communities, Piessens et al. 2004, 2005; in dry calcareous
449 grasslands communities, Evju et al. 2015) are more sensitive to the loss of structural
450 connectivity.

451
452 Therefore, it is important to develop approaches that take dispersal traits into account.
453 Such approaches are expected to complement and fill knowledge gaps on existing work based
454 on vector-types. Transposing the conceptual framework of response traits developed by Lavorel

455 et al. (1997) to landscape ecology represents a promising avenue towards understanding and
456 predicting plant community responses to changes in connectivity.

457

458 *Community weighted mean traits and functional diversity*

459 Studies over the last 15 years on community ecology have developed other methods to describe
460 the functional structure of plant communities. These methods include aggregated measures
461 quantifying the community the mean (*i.e.* community weighted mean traits) and range of trait
462 values (functional diversity, for review, see Mouchet et al. 2010). In response to local factors,
463 environmental filtering leads to convergent trait values that are adapted to environmental
464 characteristics (van der Valk 1981; Weiher and Keddy 1995; Grime 2006). In contrast, biotic
465 filtering can lead to: i) divergent trait values within communities (limiting similarity theory,
466 MacArthur and Levins 1967; Grime 2006), leading to niche differentiation, or ii) convergent
467 trait values within communities (competitive hierarchy theory, Herben and Goldberg 2014) due
468 to the competitive exclusion of less competitive species. Transposition of these theories to the
469 landscape scale is a promising research avenue in functional ecology. In response to reduced
470 connectivity, plant communities at the landscape level should be filtered toward trait syndromes
471 that promote high dispersal ability (*i.e.* low functional diversity and weighted mean trait values
472 converge toward high seed number or traits promoting long-distance dispersal).

473 Research assessing how the functional structure of communities respond at the gamma
474 scale depending on landscape characteristics is still at an early stage. To our knowledge, only
475 one study has used this highly promising approach (Favre-Bac et al. 2017b). The authors
476 demonstrated that lower ditch network connectivity induces convergent trait values toward
477 small seed production and high seed buoyancy. Higher seed buoyancy is particularly
478 favourable for successfully passing culverts, which constitute barriers (Soomers et al. 2010),
479 because seeds might persist until water level changes, wind strength or wind direction enables

480 them to continue moving downstream. In comparison, lower seed production indicates that
481 species invest heavily in vegetative growth, consolidating isolated local populations (Stöcklin
482 and Winkler 2004). By contrast, higher connectivity in ditch networks reduces this filtering
483 effect, or, even, leads to divergent trait values in seed mass. Consequently, in widely connected
484 landscapes, several strategies coexist across local communities constituting the
485 metacommunity. Higher seed weight provides more resources to guarantee growth during the
486 early stages of establishment (Cornelissen et al. 2003), which mostly depend on competitive
487 interactions with other plants within the local community. This local biotic filter favours the
488 dissimilarity of plant traits involved in harvesting resources through the niche-partitioning
489 effect (limiting similarity, MacArthur and Levins 1967; Pacala and Tilman 1994). These results
490 demonstrate that, at the gamma scale, reduced connectivity acts as a filter on the dispersal traits
491 of plant species involved in resistance to connectivity loss.

492

493 *Contribution of functional traits towards improving landscape connectivity models*

494 Trait-based studies provide a better understanding of the mechanisms involved in how plants
495 respond to connectivity. Thus, by integrating plant traits in landscape connectivity modelling,
496 a more accurate prediction of the responses of species to connectivity loss should be obtained.
497 This approach has been facilitated by the development of potential functional connectivity
498 models (Fig. 1 and Box 1) that account for species dispersal distance in addition to the cost of
499 species to cross over landscape features such as those of Pascual-Hortal and Saura (2006,
500 Integral Index of Connectivity, IIC) and Saura and Pascual-Hortal (2007, Probability of
501 Connectivity, PC). The two indices – IIC and PC – are based on different assumptions about
502 the probability of connection between two considered patches (binary or probabilistic,
503 respectively). However, only a few studies have used this type of graph-based connectivity

504 index for plants (see García-Feced et al. 2011; Aavik et al. 2014). Thus, these approaches need
505 to be generalised.

506

507 **Effect of time on the response of plants to connectivity**

508 *Historical landscape connectivity drives the taxonomic structure of plant communities*

509 Most studies have overlooked the potential effect of relaxation time when analysing the
510 influence of connectivity on plant communities. However, this effect has been detected in
511 grassland communities. For example, Helm et al. (2006) showed that the alpha richness of
512 specialist calcareous grasslands is independent of their current structural connectivity, but is
513 dependent on their connectivity 70 years ago (*i.e.* dependent on the state of the landscape before
514 drastic habitat loss and connectivity loss). These results strongly support the concept that some
515 plant communities are mostly composed of species that have the ability to resist to
516 fragmentation by persisting without completing the whole life cycle (*i.e.* with no sexual
517 reproduction stages, Eriksson 1996). Grassland plant communities are indeed mostly composed
518 of perennial plants with long-lived vegetative life-cycle, and may then survive for decades after
519 environmental changes (Eriksson 1996). Lindborg and Eriksson (2004) also detected a response
520 of alpha diversity (richness and density) to landscape structural connectivity older than 50 years
521 and 100 years ago in semi natural grasslands. The authors demonstrated an interactive effect
522 between time and spatial resolution. A positive effect of connectivity 50 years ago was only
523 detected for alpha diversity at the smaller scale (1 km radius); however, a positive effect of
524 connectivity 100 years ago was detected at both scales considered (1 km radius and 2 km
525 radius). The presence of a relaxation time following an environmental perturbation might have
526 indirect consequences on the biological scale of the response. For instance, Cousins and
527 Vanhoenacker (2011) demonstrated that the gamma diversity of semi-grassland ecosystems
528 decreases more slowly after a decline in grasslands abundance in the landscape compared to
529 alpha diversity. Although no study has yet investigated the difference in the response of alpha

530 and gamma diversity on historical connectivity, we assume that such results could be transposed
531 to connectivity loss. The time required to establish an equilibrium between spatial connectivity
532 and species richness or diversity is longer at larger spatial and biological scales compared to
533 smaller scales (O'Neill et al. 1986; Allen and Starr 1988); thus, the relaxation time of plant
534 assemblages occurs at different spatial scales.

535 To our knowledge, only Naaf and Kolk (2015) and Haddad et al. (2015) have
536 investigated how connectivity affects the magnitude of immigration credit. By studying newly-
537 established forest patches, Naaf and Kolk (2015) found that the magnitude of immigration credit
538 mainly depends on the structural connectivity of forests (IFM index). In connected forest
539 patches, immigration lag affected five forest specialist species compared to nine species in
540 highly isolated forest patches. Haddad et al. (2015) obtained similar results by studying
541 successional vegetation of pine plantations over a decade in the Savannah River Site
542 experimental design (Box 2). More specifically, immigration lags resulted in 15% fewer species
543 after a decade in unconnected patches compared to connected patches. Future studies should
544 investigate this effect in other community types.

545

546 *Dispersal traits promoting time-dependent responses to connectivity*

547 Because plants might respond to connectivity time-dependently (either with relaxation time or
548 with immigration credit), some biological traits might promote such effects. For instance, the
549 life duration of species or seed-bank persistence might contribute to the delayed response to
550 changes in connectivity. The work of Lindborg (2007) supported this assumption,
551 demonstrating that the proportion of short-lived plant species is influenced by current structural
552 connectivity, whereas that of clonal long-lived and long seed-bank persistence species is
553 influenced by historical structural connectivity (Table 1). Conversely, some traits might
554 influence the effect of immigration lag. For instance, species with poor dispersal abilities might

555 contribute strongly to immigration credit. This assumption was verified by Naaf and Kolk
556 (2015). The authors demonstrated that immigration credit is higher in species that are
557 characterised by low seed production and dispersal potential (*sensu* Vittoz and Engler 2007)
558 compared to species with high seed production and dispersal potential in forest specialist
559 communities. However, few studies have used trait-based approaches to determine how
560 connectivity changes over time.

561

562 **Effect of landscape connectivity on actual seed dispersal**

563 Studies assessing actual dispersal (Fig. 1) in response to connectivity have developed over the
564 last 15 years, but remain limited. Many papers have assessed seed fluxes at the community
565 level, particularly for water-dispersed species (*e.g.* Andersson and Nilsson 2002; Boedeltje et
566 al. 2003, 2004; Moggridge et al. 2009), but very few studies have considered the effect of
567 connectivity on these seed fluxes. Only a few studies have taken connectivity into account, with
568 the response of plants being almost exclusively assessed at the species level, which are
569 presented in the next section.

570

571 *Number of dispersed seeds*

572 The effect of connectivity on the abundance of dispersed seeds has mostly been investigated
573 under experimental conditions, focusing on particular species that were selected for their
574 abundance or representativeness of the community process. Seed fluxes for three plant species
575 dispersed by birds were assessed in connected and unconnected patches using the Savannah
576 River Site experimental design. Seeds were trapped in peripheral (*i.e.* receiver) patches, of
577 which just one was connected to the central patch and the others were not (Box 2). To provide
578 confidence that all seeds or fruits found in seed traps were exclusively derived from the central
579 patch, two methods were carried out, depending on the abundance of the species considered: i)

580 the removal of all naturally occurring individuals from the peripheral patches, and ii) the use of
581 marked seeds or fruits in the central patch by fluorescence. Based on this approach, Tewksbury
582 et al. (2002) reported that twice the number of *Ilex vomitoria* seeds was trapped in connected
583 patches compared to unconnected patches. The authors also reported that a greater proportion
584 (an increase of 18%) of *Myrica cerifera* were present in faecal samples collected in connected
585 patches that contained fluorescent powder compared to unconnected patches. Similar results
586 were obtained by Haddad et al. (2003) for both *Myrica cerifera* and *Rhus copallina*, with five
587 and two times more seeds, respectively, being transported from the central patch in connected
588 compared to unconnected patches. Using an individual-based model, Levey et al. (2005)
589 demonstrated that the distribution of *Myrica cerifera* is explained by the movement of birds
590 that were 31% more likely to be found in connected patches compared to unconnected patches.
591 Thus, it is important that future studies extend these analyses to consider other modes of
592 dispersal.

593

594 *Seed flux composition*

595 Studies analysing the seed communities of plants that actually disperse in response to landscape
596 connectivity remain scarce. To our knowledge, only one study investigated this type of
597 relationship (Suárez-Esteban et al. 2013). The authors assumed that unpaved roads act as
598 corridors, and analysed actual dispersal along unpaved roads in comparison to adjacent
599 scrubland, which was not considered to be a corridor. By analysing the seeds of all fleshy-fruit
600 shrubs that were contained in the faecal samples of frugivorous mammals, the authors
601 demonstrated that the composition of seed communities in unpaved roads differed to that
602 observed in scrublands, due to the effect of corridors on animal behaviour. However, this
603 finding was dependent on the animal-vector being considered (rabbit, carnivore or ungulate).

604 Such studies analysing actual dispersal are expected to improve the accuracy of assessing
605 current seed dispersal, allowing us to determine how connectivity influences dispersal *per se*.

606

607 **New prospects for future research**

608 Analysing the response of the plant community to connectivity loss has not been as extensively
609 studied as for animal guilds, despite the dispersal specificity of plants. Through our review, we
610 demonstrated that: i) landscape connectivity does promote the actual dispersal of plants
611 between communities (section 4), but ii) its influence on community taxonomic structure does
612 not follow a general pattern due to the many factors that modulate its effect (sections 1 and
613 3). We also found that: iii) the use of functional traits provides a better understanding of the
614 mechanisms involved in plant responses to connectivity (sections 2 and 3).

615 These three key-findings should be considered in light of several limitations related to
616 the studies selected for this review. First, this review did not compare the relative role of
617 landscape connectivity *vs.* other landscape factors (*e.g.* habitat size or habitat amount) in
618 structuring plant communities. Thus, it is beyond the scope of this review to shed light on the
619 SLOSS (Single Large Or Several Small) debate, derived from island biogeography or to discuss
620 on the relative importance between SLOSS and the Habitat Amount Hypothesis (Fahrig 2013)
621 (but see Lindgren and Cousins 2017). Secondly, the dark diversity (*i.e.* all species that are
622 absent from a habitat patch but that could disperse to and establish there, Pärtel et al. 2011) may
623 result from dispersal limitation (Riibak et al. 2015). However, the reviewed studies investigated
624 the role of landscape connectivity on expressed plant communities (*i.e.* potential dispersal, Fig.
625 1), rather than on the absence of species, neglecting the role of landscape connectivity on dark
626 diversity. Third, the consideration of traits in the response to connectivity raises a question for
627 some authors (see for example Haddad et al. 2015). These authors suggest that plant dispersal
628 might be better described by statistical probabilities and stochastic factors rather than traits.

629 Within these limitations, we identified research prospects from the three key-findings identified
630 here:

631

632 1) Landscape connectivity promotes actual dispersal between connected communities. Because
633 of the scarcity and the animal-dispersed species focus of the studies on this topic, we can only
634 encourage more studies to use this approach, particularly for other dispersal modes.

635

636 2) The influence of landscape connectivity on plant taxonomic structure do not follow a general
637 pattern because of the multiplicity of factors that modulate its effect. To better disentangle the
638 effect of landscape connectivity from the other factors, explicit consideration of both spatial
639 and temporal scales is necessary to define a relevant resolution of the landscape. An assessment
640 of landscape connectivity at different spatial scales should be developed to detect the dispersal
641 range at which plant species respond to changes in connectivity. Because some species exhibit
642 a time lag in their response to connectivity changes, efforts to incorporate historical data to
643 model historical connectivity are necessary. In addition, the presence of a corridor *per se* is not
644 sufficient to connect habitats. Indeed, the quality of the corridors (or landscape elements) should
645 be considered and determined by their management practice. For instance, in hedgerows, the
646 corridor quality is determined by the vegetation structure and vertical organisation at a fine
647 scale. The assessment of connectivity might account for these fine-scale characteristics by using
648 recent remote sensing techniques (Betbeder et al. 2014) to better predict species abundance
649 such as for carabids (Betbeder et al. 2015). Future studies should investigate this new
650 methodology for plants. Connectivity might be evaluated while considering the potential
651 interaction between habitats, to better account for the degree of ecological specialisation of
652 species. Complementarity between the different ecological corridor types (*i.e.* provided by
653 different habitat types) might explain the lowest sensitivity of generalist species to connectivity

654 loss. In contrast, antagonistic effects might occur for specialist species. The deployment of such
655 multi-habitat landscape connectivity models (which independently consider different
656 ecological corridor types) could enhance our understanding of the responses of plant species to
657 connectivity at a community scale.

658

659 3) Using functional traits provides a better understanding of the mechanisms involved in plant
660 responses to connectivity. Some trait syndromes characterise species that are highly sensitive
661 to connectivity loss. Determining trait combinations that might predict, at best, plant responses
662 in time and space to changes in connectivity is a key challenge of forthcoming research. Using
663 such functional indicators would allow these species to be detected in a manner that is
664 reproducible and independent of ecosystems and regional pools (Lavorel et al. 1997). This
665 approach is promising for defining general functional indicators of sensitivity. Such indicators
666 may, for instance, help to identify species that are less likely to colonise and establish in patches
667 after connectivity loss. In addition, the use of functional connectivity indices, which considers
668 the dispersal distance of species, should be generalized in studies investigating plants,
669 especially at the community level. The dispersal traits that promote time-dependent responses
670 to connectivity that we have identified should be integrated in these indices to provide an
671 adequate understanding of connections between plant communities over time.

672

673 Beyond highlighting needs for future research, this synthesis provides information of use for
674 land-use planning (green and blue infrastructure implementation, for instance, Sandström 2002;
675 Tzoulas et al. 2007). Such information could provide new methods and decision-making tools
676 to promote the operational establishment of ecological corridors, taking plant communities into
677 account.

678

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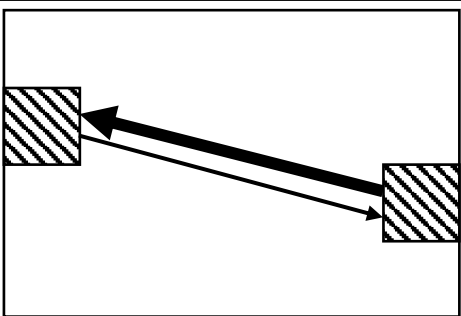
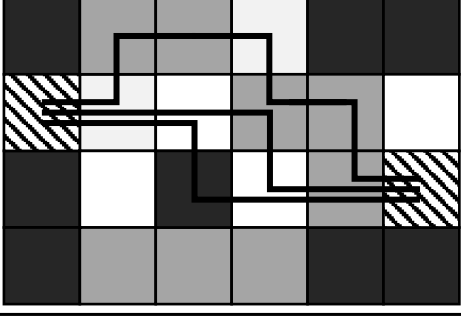
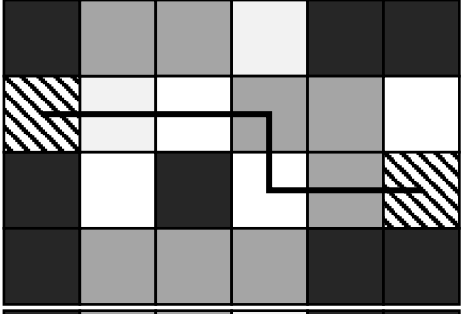
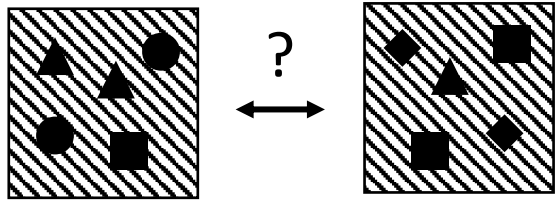
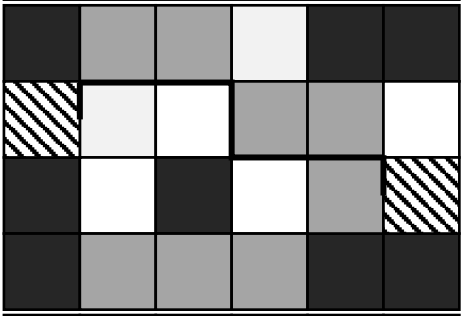
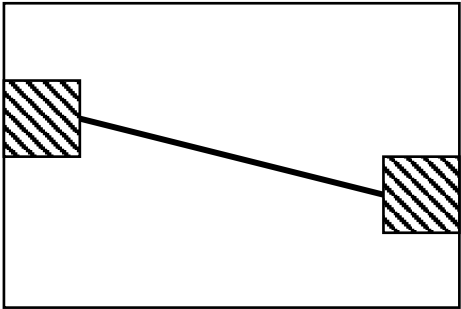
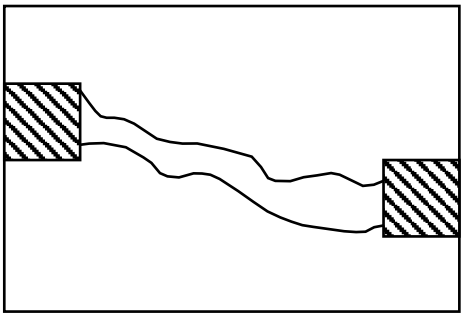
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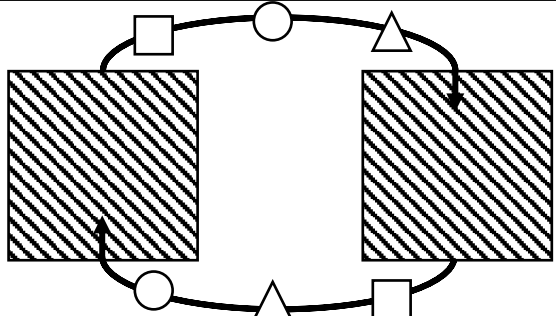
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1062 **Fig. 1** Methods used to determine how landscape connectivity influences plant dispersal. (A)
1063 Study of potential dispersal (*i.e.* results of seed bank expression in habitat patches, integrating
1064 hence the local establishment process). White squares with diagonal lines represent focal habitat
1065 patches (patches of interest). Solid squares, triangles, circles and rhombus represent different
1066 plant species. Four measures of connectivity are employed: (1) *Presence/absence of corridors*;
1067 (2) *Euclidian distance*; (3) *Structural connectivity* and (4) *Potential functional connectivity*.
1068 White squares represent landscape elements of the same habitat type than the focal habitat
1069 patches. Grey and black squares represent two different types of habitat patches. To determine
1070 potential functional connectivity, two different modelling approaches are commonly employed:
1071 (4*) *least-cost path* and (4**) *circuit theory*. Both methods require parameterising resistance
1072 surfaces, with cost value reflecting the cost of species to traverse landscape features. In these
1073 cases, assigned costs to landscape features increase from white (highly permeable to dispersal)
1074 to black (slightly permeable to dispersal). (B) Study of actual dispersal (*i.e.* seed rain) White
1075 squares with diagonal lines represent habitat patches. Solid squares, triangles, circles and
1076 rhombus represent the seeds of different plant species. One measure of connectivity is
1077 employed: (5) *Actual functional connectivity*. Thicker arrows represent a higher rate of dispersal
1078 (*i.e.* higher connectivity), while thinner arrows represent a lower rate of dispersal (*i.e.* lower
1079 connectivity).

A



B



Box 1 Glossary

Structural connectivity: measure of connectivity based on the spatial position of patches independent of the attributes of the organism of interest (Tischendorf and Fahrig 2000; Bennett 2003; Taylor et al. 2006).

Potential functional connectivity: measure of connectivity that combines the physical attributes of the landscape with limited information about dispersal ability (Calabrese and Fagan 2004). This measure explicitly considers the behavioural responses of organisms to the physical structure of the landscape (Tischendorf and Fahrig 2000; Bennett 2003; Taylor et al. 2006).

Least-cost paths: modelling method to determine potential functional connectivity that assumes a unique path between two patches (represented by a solid line in Fig. 1), hypothesising that individuals perceive their environment in a way that leads them to “select” the optimal path (Adriaensen et al. 2003). The connectivity measure that results from this modelling method is an isolation measure called least-cost distance: the higher the least-cost distance, the lower connectivity.

Circuit theory: modelling method to determine to determine potential functional connectivity that evaluates all possible paths (represented by the three different solid lines in Fig. 1), assuming that dispersal follows random walks. The connectivity measure that results from this modelling method is an isolation measure called resistance distance: the higher the resistance distance, the lower connectivity (McRae et al. 2008).

Actual functional connectivity: measure of connectivity based on the observation of individuals moving through a landscape (Calabrese and Fagan 2004). This measure explicitly considers the behavioural responses of organisms to the physical structure of the landscape (Tischendorf and Fahrig 2000; Bennett 2003; Taylor et al. 2006).

Box 2 Example of the Savannah River Site (SRS) experimental design for connectivity studies.

This experimental design is located in the Savannah River Site, a National Environmental Research Park in South Carolina, USA.

In 2000, eight 50-hectares landscapes were selected. These landscapes were composed of mature (40- to 50-year-old) forest, dominated by loblolly pine (*Pinus taeda*) and longleaf pine (*Pinus palustris*).

Within each landscape, five early-

successional habitat patches were created by cutting and removing all trees, and then burning the cleared areas. The patches included (Fig. 2): one central patch of 1 ha (A) and four peripheral patches (B, C, D, E) that were equal in distance (150 m) from the central patch, but with different structures (see below).

The experiment focused on two corridor functions. First, how a corridor impact connectivity through the following configuration: the central patch is connected to one peripheral patch (B) by a 150 m long and 25 m wide corridor and is not connected to the three other peripheral patches (B, C, D). The three other peripheral patches are equal in area to a patch plus a corridor (1.375 ha). Second, how a corridor impacts patch shape through the following manipulation of peripheral patches: in four landscapes, two of the remaining three peripheral patches were winged (C and D) and one was rectangular (E); in the other four landscapes, two peripheral patches were rectangular and one was winged.

The number of experimental landscapes used varied from six (Damschen et al. 2006) to eight (Tewksbury et al. 2002; Haddad et al. 2003, 2015; Levey et al. 2005; Damschen et al. 2008; Brudvig et al. 2009). This number was not clarified in Haddad et al. (2003).

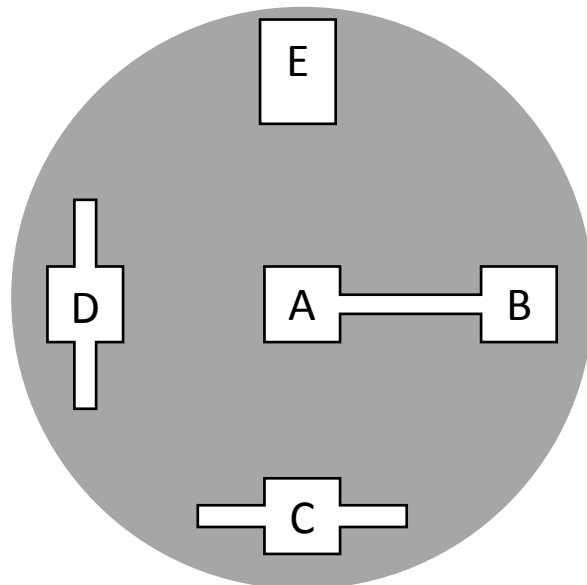


Fig. 2 One of the eight experimental landscapes in the SRS.

In our review, only the connectivity function of the corridor is discussed; thus, we only refer to connected patches *versus* unconnected patches.

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1084 **Table 1** Synthesis of studies dealing with the effect of current and historical landscape connectivity on functional structure of plant communities.

1085 See Fig.1 for detailed explanations on the connectivity measures.

Approach	Community type	Connectivity measure	Community variable	response	Main results	Reference
Experimental	Early successional vegetation of large pine plantations	Connected vs. unconnected patches (during 7 years)	Difference in species richness	alpha	↗→ for animal dispersed species ↗ for wind dispersed species ↗ for unassisted species	Damschen et al. (2008)
Correlative	Field margins, road verges & ditches	Euclidian distance Potential connectivity: least-cost and resistance distance	Jaccard similarity		∅ for animal and wind dispersed species ↘ for unassisted species	Thiele et al. (2017)
Correlative	Ditches	Structural connectivity: Total ditch length (TDL) Number of culverts (NoC) Number of intersections (NoI) Number of subunits (NoS)	Gamma richness similarity Species trait values: Seed mass Seed buoyancy Seed morphology Seed velocity Seed germination	and	∅ for water-dispersed species ↘ (TDL); ∅ (NoC); ↗ (NoI) ∅ (TDL); ↗ (NoC, NoI) ↗ species with round seeds (TDL); ↗ species with long seeds (NoC, NoI) ↘ (TDL); ∅ (NoC); ↗ (NoI) ↘ (TDL); ∅ (NoC); ↗ (NoI)	Favre-Bac et al. (2014) Favre-Bac et al. (2017a)
			Standard effect size values calculated for Rao's quadratic entropy and gamma scale weighed mean trait values Seed production Seed buoyancy Seed mass		∅ (TDL, NoC); ↘ Convergence toward the production of small seeds (NoI); ↗ Convergence (NoS) toward the production of small seeds ∅ (TDL; NoI; NoS); ↗ Convergence toward a high buoyancy (NoC) ↗ Divergence (TDL); ∅ (NoC, NoI, NoS);	Favre-Bac et al. (2017b)

Correlative	Temperate forests	Structural connectivity (IFM index)	Trait values of emergent groups to connectivity loss	Sensitive emergent group: Unassisted dispersal Few and heavy seeds High clonality Short seed bank longevity Small height	Resistant emergent group: Assisted dispersal Many and thin seeds No or little clonality Long seed bank longevity Tall	Kolb and Diekmann (2005)
Correlative	Grasslands	Structural connectivity (IFM index)	Species richness of emergent groups	↗ for perennial rosette ∅ for orchids, half-rosette and annuals species		Adriaens et al. (2006)
Correlative	Dry calcareous grasslands	Structural connectivity (IFM index)	Probability of occurrence in response to connectivity	↗ for species with low seed number ∅ for species whatever their dispersal mode (wind-dispersal or not), seed mass or seed bank longevity ↗ for short-living species ∅ for clonal species		Evju et al. (2015)
Correlative	Heathlands	Structural connectivity (IFM index)	Species richness in the different categories of the seed longevity index	↗ for species with short seed bank longevity		Piessens et al. (2004)
Correlative	Heathlands	Structural connectivity (IFM index)	Regression coefficient resulting from the logistic regression between patch occupancy for each species as explained by connectivity intensity	↗ for species with short seed bank longevity ∅ for species whatever their mean plant height, seed mass, dispersal mode, growth form, self-compatibility, clonal growth form and seed number		Piessens et al. (2005)

Correlative	Temperate forests	Structural connectivity (modified version of IFM index that incorporates patch age)	Regression coefficient resulting from the logistic regression between patch occupancy for each species as explained by connectivity intensity	↗ for vertebrate and wind-dispersed species ↗ for species with low seed production ↗ for species with small height ∅ for species whatever their life cycle duration	Verheyen et al. (2004)
Correlative	Urban - ruderals	Structural connectivity (IFM index)	Trait values of response groups to connectivity: Terminal velocity Number of seeds Seed mass	Sensitive > resistant species Sensitive < resistant species Sensitive = resistant species	Schleicher et al. (2011)
Correlative	Grasslands	Current (C) and historical (H) structural connectivity (IFM index) 1 km radius 2 km radius	Proportion of species	∅ for animal-, wind- dispersed and unassisted species ∅ for species whatever their seed size ∅ (C); ↘ (H) for long seed bank persistence species ↗ (C); ∅ (H) for annual plants ∅ (C); ↘ (H) for perennials with or without clonality at 1 km scale. ∅ (C) for perennials with or without clonal ability at 2 km scale ↘ (H) for perennials without clonal ability at 2 km scale	Lindborg (2007)

1087 **Effect of landscape connectivity on plant communities: a review of response patterns**

1088

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1094 **Appendix S1 Methods**

1095

1096 We systematically reviewed articles to assess whether and how landscape connectivity affects
1097 the assembly of plant communities. Using Web of Science and Google Scholar to gather
1098 publications using the following keywords: landscape connectivity, habitat isolation, corridors
1099 and plants. Because ecosystem functioning is completely different in tropical systems, we
1100 excluded these studies, only considering studies conducted in temperate systems. We also
1101 excluded studies that focus on fragmentation (*i.e.* that are conducted in a fragmented landscape
1102 context); that is, when it is not possible to disentangle the effects of decreased connectivity
1103 (variable of interest) and decreased habitat area. We only considered studies that: i) manipulated
1104 connectivity through the presence (or absence) of an experimentally-created corridor between
1105 two habitat patches for experimental approaches, and ii) measured connectivity in a quantitative
1106 manner (*via* the use of indices) for correlative approaches. Quantitative connectivity
1107 assessments were based on isolation metrics such as Euclidean distance, structural connectivity
1108 indices (see various examples in the main text), least-cost distance or resistance distance. We
1109 selected studies that focused on how landscape connectivity affected plants at the community
1110 level. Within this framework, we included studies with taxonomic approaches (*i.e.* looking at
1111 the composition and diversity of plant communities) and trait-based approaches (*i.e.* looking at
1112 the composition and diversity of traits). These studies assessed plant community response
1113 through: i) analysis of individual species responses across most species at the community level,
1114 and ii) aggregated measures across most species of a community. More specifically, only the
1115 following measures were extracted from articles that provided: i) taxonomic and ii) trait-based
1116 approaches:

1117

1118 i) Taxonomic approaches: alpha diversity (species richness, species density or species
1119 abundance), beta diversity (Jaccard similarity index) and gamma diversity (gamma
1120 species richness)

1121 ii) Trait-based approaches:

1122 a. Dispersal mode approach: analyses similar to the taxonomic approach but per
1123 dispersal mode, proportion of species per dispersal mode and indicators for
1124 species sensitivity to connectivity (probability of occurrence in response to
1125 connectivity, regression coefficient resulting from the logistic regression
1126 between patch occupancy for each species as explained by connectivity
1127 intensity)

1128 b. Emergent groups approach: trait values of emergent groups and species richness
1129 of emergent groups

1130 c. Response traits approach: indicators for species sensitivity to connectivity
1131 (probability of occurrence in response to connectivity, regression coefficient

1132 resulting from the logistic regression between patch occupancy for each species
1133 as explained by connectivity intensity), species richness in the different
1134 categories of the seed longevity index, proportion of species characterised by a
1135 trait, trait value of response groups to connectivity and species trait values
1136 d. Community weighted mean traits and functional diversity approach: functional
1137 gamma diversity (standard effect size values calculated for Rao's quadratic
1138 entropy traducing functional divergence or convergence) and gamma aggregated
1139 mean trait values (gamma scale weighed mean trait values, indicating the mean
1140 value towards which traits converged)

1141

1142 Concerning actual dispersal approaches, we included studies at the species level because very
1143 few studies have assessed the actual dispersal of communities in relation to connectivity.

1144