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► To cite this version:

Léa Uroy, Aude Ernoult, Cendrine Mony. Effect of landscape connectivity on plant communities a review of response patterns. *Landscape Ecology*, 2019, 34 (2), pp.203-225. 10.1007/s10980-019-00771-5 . hal-02050502

HAL Id: hal-02050502

<https://univ-rennes.hal.science/hal-02050502>

Submitted on 13 Mar 2019

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Title:

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

Uroy L.¹, Ernoult A.¹, Mony C.¹

¹: UMR CNRS ECOBIO, University of Rennes, Avenue du Général Leclerc, 35042 Rennes
Cedex, France

Corresponding author information:

Léa Uroy

Phone number: (+33)6.34.25.62.22

E-mail address: lea.uroy@univ-rennes1.fr

Abstract:

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

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

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

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

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

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

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

Introduction

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

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

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

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

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

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

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

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

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

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

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

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

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

Contrasted effect of landscape connectivity on plant community taxonomic structure

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

Plant community diversity

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

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

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

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

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

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

Plant community composition

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

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

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

Effect of landscape connectivity on the functional structure of plant communities

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

Dispersal vector mode

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

Animal-dispersal is oriented, and depends on animal behaviour and movement in the landscape. There is broad consensus that animal movement is facilitated by landscape connectivity (Murphy and Lovett-Doust 2004; Haddad and Tewksbury 2006; Gilbert-Norton et al. 2010; Haddad et al. 2011, 2015; Fletcher et al. 2016); thus, animal-dispersed plant species might be largely dependent on landscape connectivity. It is more difficult to predict how connectivity affects wind-dispersed plants, as this type of dispersal is made at random or occurs in relation to the dominant wind direction. Differences in these two plant dispersal vectors might lead to different responses to connectivity. Damschen et al. (2008) surveyed the species richness of bird-dispersed and wind-dispersed species over a seven-year period in the Savannah River Site (Box 2). The authors demonstrated that, for both functional groups, the richness of communities was lower in unconnected versus connected patches. However, this difference in 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

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

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

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

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

Plant dispersal traits

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

Emergent groups to connectivity

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

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

Response traits to connectivity

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

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

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

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

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

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

Community weighted mean traits and functional diversity

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

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

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

Contribution of functional traits towards improving landscape connectivity models

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

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

Effect of time on the response of plants to connectivity

Historical landscape connectivity drives the taxonomic structure of plant communities

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

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

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

Dispersal traits promoting time-dependent responses to connectivity

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

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

Effect of landscape connectivity on actual seed dispersal

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

Number of dispersed seeds

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

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

Seed flux composition

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

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

New prospects for future research

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

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

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

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

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

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

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

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

679 **Acknowledgements**

680 This work was funded by the Fondation de France (BISCO project). We thank the two
681 anonymous referees for their constructive work and remarks on the manuscript.

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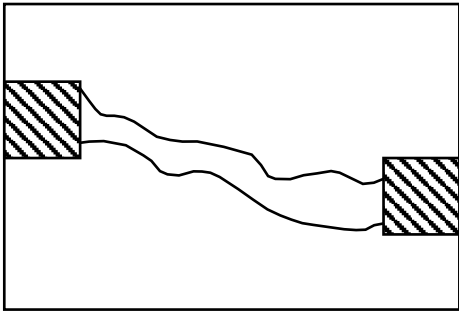
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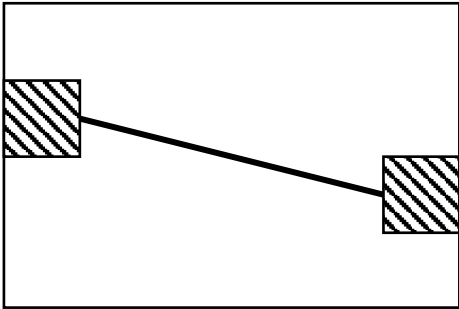
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Fig. 1 Methods used to determine how landscape connectivity influences plant dispersal. (A) Study of potential dispersal (*i.e.* results of seed bank expression in habitat patches, integrating hence the local establishment process). White squares with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

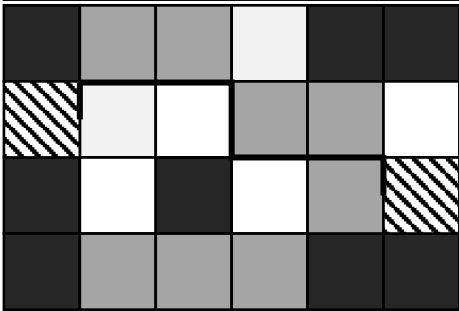
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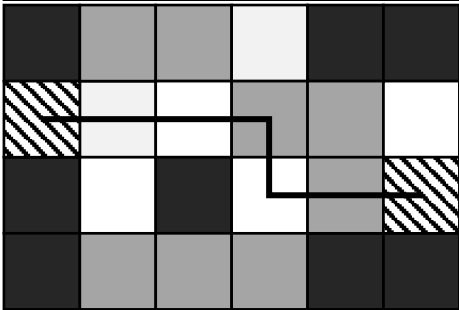
(1)



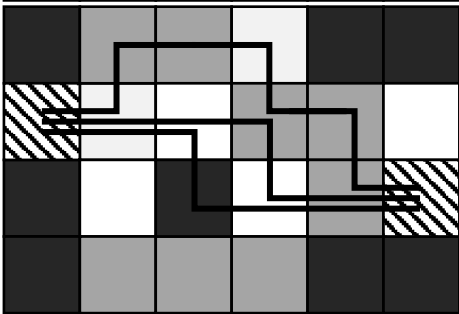
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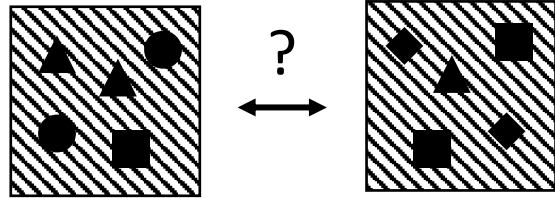
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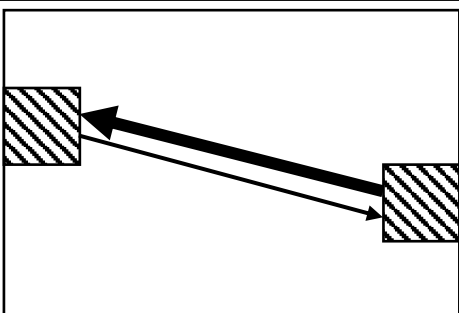
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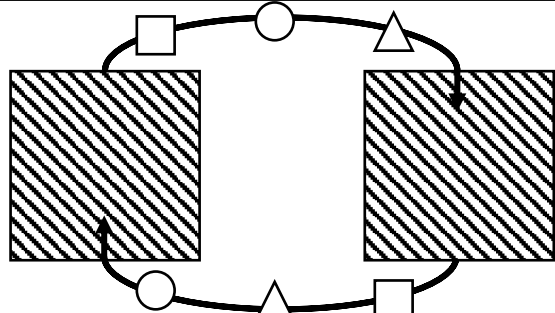
(4**)



B



(5)



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 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*).

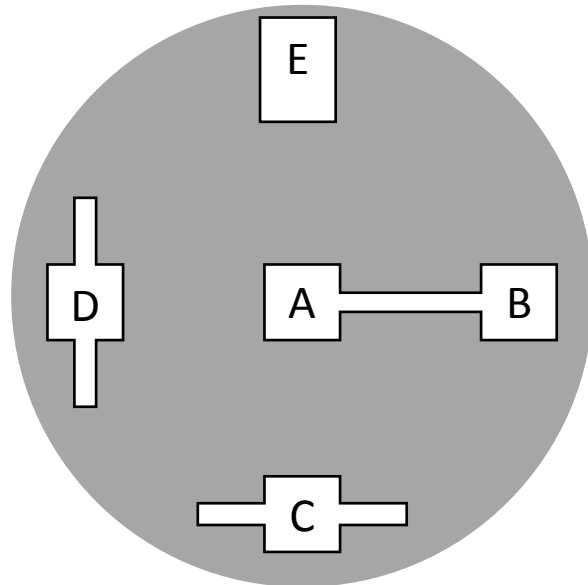


Fig. 2 One of the eight experimental landscapes in the SRS.

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).

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

1082

1083

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 and similarity Species trait values: Seed mass Seed buoyancy Seed morphology Seed velocity Seed germination Standard effect size values calculated for Rao's quadratic entropy and gamma scale weighed mean trait values Seed production Seed buoyancy Seed mass		∅ 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) ∅ (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. (2014) Favre-Bac et al. (2017a) Favre-Bac et al. (2017b)

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

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

Uroy L.¹, Ernoult A.¹, Mony C.¹

¹: UMR CNRS ECOBIO, University of Rennes, Avenue du Général Leclerc, 35042 Rennes Cedex, France

Appendix S1 Methods

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

- i) Taxonomic approaches: alpha diversity (species richness, species density or species abundance), beta diversity (Jaccard similarity index) and gamma diversity (gamma species richness)
- ii) Trait-based approaches:
 - a. Dispersal mode approach: analyses similar to the taxonomic approach but per dispersal mode, proportion of species per dispersal mode and indicators for species sensitivity to connectivity (probability of occurrence in response to connectivity, regression coefficient resulting from the logistic regression between patch occupancy for each species as explained by connectivity intensity)
 - b. Emergent groups approach: trait values of emergent groups and species richness of emergent groups
 - c. Response traits approach: indicators for species sensitivity to connectivity (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