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# ECOGRAPHY

## Review

### Landscape connectivity for the invisibles

Cendrine Mony, Léa Uroy, Fadwa Khalfallah, Nick Haddad and Philippe Vandenkoornhuys

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Because of land use changes, a worldwide decrease in biodiversity is underway, mostly driven by habitat degradation and fragmentation. Increasing landscape connectivity (i.e. the degree to which the landscape facilitates movement between habitat patches) has been proposed as a key landscape-level strategy to counterbalance the negative effects of habitat fragmentation. A robust theoretical and methodological framework has been developed for the concept of connectivity, and an increasing body of empirical evidence supports the relevance of connectivity for biodiversity. However, the framework was built ignoring species that represent the dominant proportion of biodiversity on earth: microorganisms. The extent to which the existing conceptual and methodological frameworks on connectivity can be applied to microorganisms remain unknown. We reviewed existing evidence and analyzed methods to test the influence of connectivity on microorganisms. We included all types of microorganisms, from symbiotic to pathogenic and free-living microorganisms, across all ecosystems. We describe the effect of connectivity on microorganism populations and communities, and identify the limitations and large gaps in current knowledge. Microorganisms can differ from macroorganisms in their response to connectivity due to short (distance less than a meter) dispersal distance of some groups, longer time lag of microorganisms response (possibly accompanied by evolutionary processes) and host association. The latter relies on tight interactions and feedback effects that drive microbial-landscape relationships and lead to possible coadaptation processes. Incorporating the connectivity concept in microbial community assembly rules to preserve the diversity of microbial communities and the ecosystem services they provide could be a crucial step forward in the face of pressing global changes.

Keywords: corridors, dispersal, habitat fragmentation, landscape ecology, microbial species assembly, microorganisms

#### Introduction

Biodiversity is declining so rapidly that we are in the midst of a sixth extinction crisis (Barnosky et al. 2011, Kolbert 2014, Ceballos et al. 2015). Habitat degradation and



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fragmentation are considered to be the main drivers of the decline. These processes reduce the availability of favorable habitat patches (Box 1) by reducing patch area and increasing patch isolation (Haddad et al. 2015). In this context, theory has been motivated by – and empirical studies have tested – macroorganisms’ response to landscape change. To mitigate the negative effects of habitat fragmentation, linear strips of habitat (habitat corridors), series of discontinuous small patches (stepping-stones) and highly permeable landscape matrixes connecting otherwise isolated habitat patches have been proposed as key strategies to increase landscape connectivity (Box 1; Hilty et al. 2006). Connecting habitat patches is assumed to facilitate dispersal (Rosenberg et al. 1997, Beier and Noss 1998), thereby increasing genetic fluxes (Wilson and Willis 1975) and rescuing local populations from extinction (rescue effect; Box 1; Brown and Kodric-Brown 1977, Rosenberg et al. 1997, Beier and Noss 1998). Meta-analyses have demonstrated a generally positive effect of connectivity on dispersal, abundance, genetic diversity and species richness in macroorganisms (Beier and Noss 1998, Gilbert-Norton et al. 2010, Fletcher et al. 2016), while negative effects are possible (Haddad et al. 2014).

Whereas studies of macroorganisms’ responses to connectivity have enabled notable progress in understanding its effects, the role of connectivity in microbial communities is still overlooked. New research on microorganisms would advance our knowledge of the effects of connectivity on ecosystems. If the theory developed for macroorganisms also applies to microorganisms, then the impacts of higher connectivity would have an even more important role in limiting the effect of habitat fragmentation on ecological systems. The diversity of microorganisms vastly exceeds that of macroorganisms (Mora et al. 2011). These microorganisms provide a wide range of ecosystem services including soil fertility (Adhikari and Hartemink 2016, Guo et al. 2019), food

production, plant and animal health (McKenney et al. 2018) and water purification (Adhikari and Hartemink 2016). Human activities, especially in agriculture, have the potential to reduce microbial diversity (Wang et al. 2018, Xu et al. 2020). Whether the global biodiversity crisis demonstrated for macroorganisms is likely to downscale to this microbial ‘invisible’ biodiversity is not known (Thaler 2021), but if so, it should lead to significant changes in the associated provision of services (Delgado-Baquerizo et al. 2016, Wang et al. 2018).

The effect of dispersal on microbial distribution has been observed by analyzing the biogeographic patterns of microorganisms (Martiny et al. 2006, Hanson et al. 2012). The role of dispersal in species assembly has been formalized through the metacommunity framework and applied to microorganisms (Langenheder and Lindström 2019). The metacommunity theory predicts species coexistence from the rate of dispersal, the heterogeneity of habitat patches and the species niche and fitness (Leibold et al. 2004, Logue et al. 2011). It shows that 1) intermediate dispersal results in the highest diversity at the community scale and 2) between-community and regional diversity decline as dispersal increases because of increased homogenization of the metacommunity (Mouquet and Loreau 2003). Dispersal rates depend to a great extent on landscape connectivity (sensu Taylor et al. 1993; Box 1). Yet, the effect of connectivity on microorganism dispersal remain poorly known. In microorganisms, dispersal is either active (i.e. achieved through cilia or flagella) or passive (i.e. through vectors) leading to contrasted dispersal distances. Dispersal distances may range from centimeters to hundreds of meters in the case of bacteria (Horner-Devine et al. 2004, Yang and van Elsland 2018) and fungi (Peay et al. 2010). The traits of microorganisms, such as their small size or their very high dispersal capacity, differ from those of macroorganisms in ways that may affect the ability of current theory to predict microbial responses to habitat connectivity.

### Box 1: Main definitions

*Habitat patches:* Discrete areas of ‘homogeneous’ environmental conditions where the patch boundaries are distinguished by discontinuities in environmental character states from their surroundings at magnitudes that are perceived by – or relevant to – the organism or ecological phenomenon under consideration (Wiens 1976, Kotliar and Wiens 1990).

*Landscape connectivity:* The degree to which the landscape facilitates or prevents movement, and especially dispersal movements, among habitat patches (Taylor et al. 1993).

*Rescue effect:* The effect due to migrants. Increased colonization increases population size (demographic rescue) and persistence (genetic rescue), thereby preventing local extinction (Brown and Kodric-Brown 1977). The microbial rescue effect is the ability of modified microbial communities (microbiota) to increase their host fitness and population densities, thereby preventing host extinction (Mueller et al. 2020).

*Scale of effect:* Spatial extent at which landscape structure best predicts microorganism responses (Jackson and Fahrig 2012, 2015).

*Cross habitat spillover:* The movement of organisms from one habitat type to another for the purpose of dispersal and/or foraging (Tscharrntke et al. 2012).

*Extinction debt:* The number of species yet to go extinct in the patch following a loss of connectivity (Figueiredo et al. 2019). This time-lag represents the delay in species response to environmental change (Tilman et al. 1994).

*Colonization credit:* The number of species yet to colonize a patch following a gain in connectivity (Cristofoli et al. 2010). Time delay reflects a lag in immigration lag, which leads to immigration credit (Kuussaari et al. 2009).

The size-dispersal hypothesis indeed predicts that smaller organisms are more likely to be affected by species-sorting (i.e. changes in the community related to patch quality and to the local demography of species and making it possible to fit to environmental gradients (Leibold et al. 2004)) than by dispersal limitation. Such predictions rely on the assumption that smaller organisms disperse over longer distances than macroorganisms thereby reducing the intensity

of the dispersal filter (Cottenie 2005, Beisner et al. 2006, Shurin et al. 2009). Microorganisms usually also produce large numbers of propagules, many more than macroorganisms, which would increase mass effects (i.e. competitive exclusion balanced by immigration; (Leibold et al. 2004). For instance, in ectomycorrhizal fungi, production is estimated at billions to trillions of spores (i.e. tiny propagules) per km<sup>2</sup> (Peay et al. 2012). Despite limited knowledge of the dispersal

Table 1. Research questions, predictions and knowledge gaps.

Research questions	Predictions	Knowledge gaps on microorganisms
How are microorganisms affected by connectivity?	<ul style="list-style-type: none"> <li>• Increased dispersal (Rosenberg et al. 1997)</li> <li>• Richness is affected depending on the relative rate of dispersal (Metacommunity framework; Leibold et al. 2004)</li> <li>• Small species are less-dispersal limited (Size-hypothesis applied to small species or species with passive dispersal; Cottenie 2005, Beisner et al. 2006, Shurin et al. 2009)</li> </ul>	<ul style="list-style-type: none"> <li>• Most existing studies are on pathogens species, with indirect quantification of population abundance (i.e. symptoms)</li> <li>• No study of rare species exists despite their huge proportion in microbial total richness</li> <li>• There have been very few studies at the community level</li> <li>• All studies have been on corridors, even though it is not the most widely distributed type of connectivity in nature</li> </ul>
How do dispersal traits interact with responses to connectivity?	<ul style="list-style-type: none"> <li>• Connectivity affects passive dispersal through the effect of connectivity on dispersal vectors</li> <li>• Active dispersal might be affected by connectivity but at a short spatial scale owing to the short dispersal distance</li> </ul>	<ul style="list-style-type: none"> <li>• Lack of knowledge on dispersal traits for microorganisms</li> <li>• Very few studies have investigated the interaction between dispersal traits and response to connectivity, even within a given taxonomic group</li> </ul>
What mechanisms underlie the effect of connectivity?	<ul style="list-style-type: none"> <li>• Connectivity increases dispersal (Beier and Noss 1998, Haddad et al. 2011)</li> <li>• Connectivity effects can be confused with edge or habitat amount effects in corridors</li> </ul>	<ul style="list-style-type: none"> <li>• Very few studies have tested the mechanisms behind a response to landscape connectivity</li> <li>• For corridors, there is a need to disentangle the effect of connectivity on dispersal from the other effects.</li> <li>• Need to better describe the processes underlying edge effects in microorganisms</li> <li>• Need to better understand the particular case of biotic connectivity in which host-microbiota interactions are thought to be an important driver</li> </ul>
What are the best predictors to assess landscape connectivity for microorganisms?	<ul style="list-style-type: none"> <li>• Functional predictors are assumed to be better than structural predictors or geographical distance, as they take more realistic dispersal pathways into account</li> </ul>	<ul style="list-style-type: none"> <li>• Most existing literature focuses on isolation by distance</li> <li>• Some studies on structural connectivity based on the habitat/non habitat conceptual landscape model</li> <li>• Need to develop functional connectivity predictors</li> <li>• Few studies test the scale of effect</li> </ul>
What is the scale of effects for microorganisms?	<p><i>In space</i></p> <ul style="list-style-type: none"> <li>• Scale depends on body size (Holland et al. 2005, Thornton and Fletcher 2014 but see Jackson and Fahrig 2015 for independent effects)</li> </ul> <p><i>In time</i></p> <ul style="list-style-type: none"> <li>• Scale depends on the biological traits of the species (generation rate, traits involved in species survival; Figueiredo et al. 2019)</li> </ul>	<ul style="list-style-type: none"> <li>• Most studies are conducted at the landscape scale (i.e. from hundreds of meters to kilometers), and very few at the scale of less than a meter</li> <li>• Need to analyze nested-scales of connectivity – from short to large spatial scales</li> </ul>
How can microorganisms be taken into account when creating corridors?	<ul style="list-style-type: none"> <li>• Connectivity has to be preserved and restored between biodiversity hotspots</li> </ul>	<ul style="list-style-type: none"> <li>• Define what we consider hotspots for microorganisms</li> <li>• Establish connectivity at multiple spatial scales to account for the range of scales of microorganism response to habitat fragmentation</li> <li>• Test the microbial rescue effect due to corridor implementation</li> <li>• Consider host and its microbiota as a single entity for corridor implementation</li> </ul>

of microorganisms, it appears that the production of so many propagules is offset by the fact that the vast majority of spores fall close to their emission source (Galante et al. 2011) and by the very low probability of achieving viable germination (Peay et al. 2012). Lastly, microorganisms usually have a short generation time ranging from minutes to at the most, a few days. Dispersal over kilometers can then happen very quickly, even if it is over many generations. Because of these differences between micro- and macroorganisms, the effect of connectivity on microbial assemblages may differ.

In this review, we investigate whether connectivity affects microorganism distribution, determine to what extent the underlying mechanisms and processes resemble those observed in macroorganisms, and underline the gaps in the knowledge needed before applying current conceptual models to microorganisms (Table 1). To obtain a general overview, we included all types, i.e. symbiotic, pathogens and free-living microorganisms, across aquatic to terrestrial ecosystems. In the following, the spatial extents considered are close to the classical spatial scales of macroorganisms – from hundreds of meters to kilometers. We excluded larger scales (continental or ocean spatial extents), we considered to be irrelevant regarding the range of dispersal distances of microorganisms. Smaller spatial extents – of less than a meter – are discussed in a dedicated section ('Micro-connectivity for microorganisms').

## Connectivity in landscapes

### Improving non-biotic connectivity: from habitat linkages to the surrounding landscape

Non-biotic connectivity can be improved by three types of strategies depending on the landscape conceptual model used. The first category of conceptual models is a binary view of the landscape, composed of habitat patches embedded in an inhospitable matrix of non-habitat (the 'island' model; MacArthur and Wilson 1967). This 'island' model was then extended and supplanted by the 'patch–corridor–matrix' model (Forman 1995; Fig. 1), which includes the presence of corridors and stepping-stones (Fig. 1). Corridors are not easy to find in nature (but see the particular case of river networks connecting aquatic elements or hedgerow networks connecting forest patches). Situations that are more common include discontinuous habitat patches distributed in the matrix (stepping-stones). The more recently developed 'landscape mosaic' model (Wiens 1995) recognizes that landscape mosaics are heterogeneous and comprise patches of different habitat types, which vary in their degrees of permeability to the movement of organisms (Murphy and Lovett-Doust 2004). Connectivity is thus dependent on the heterogeneity of the entire landscape matrix (Fig. 1). In microbial studies, most works have considered corridors, either through the use

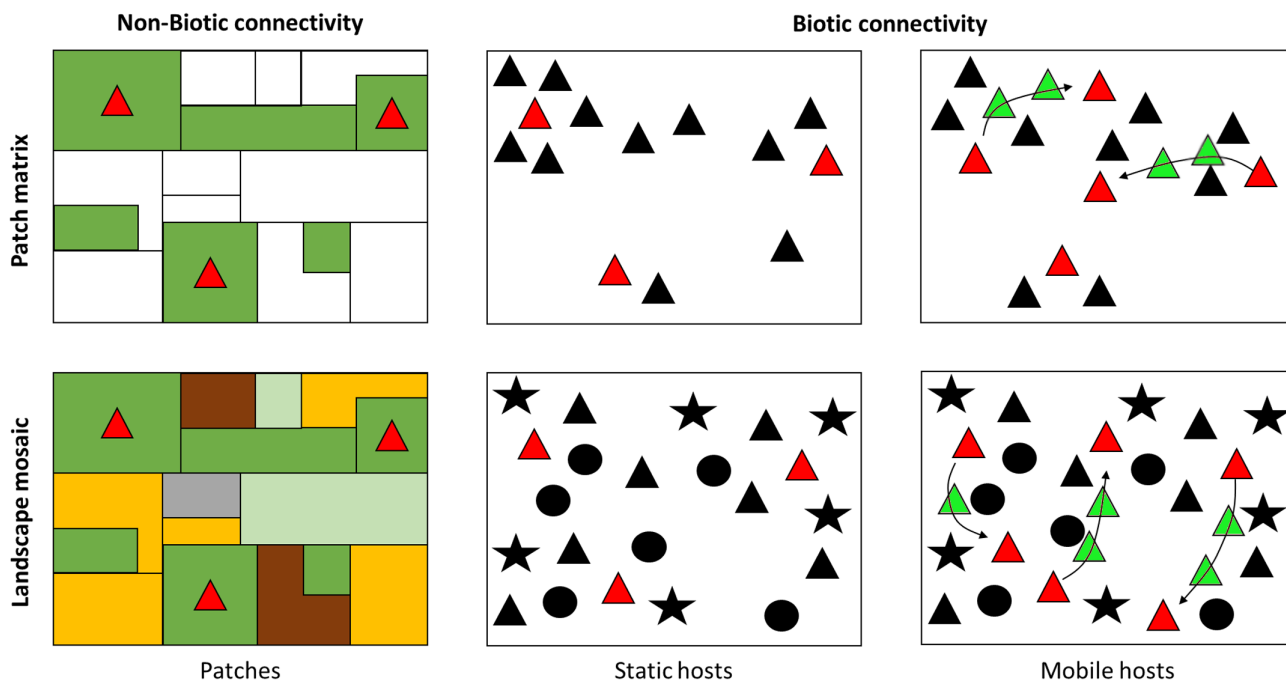


Figure 1. Representation of the types of connectivity for microorganisms (non-biotic versus biotic connectivity) in relation to the landscape conceptual model. Non-biotic connectivity is the degree to which the abiotic landscape facilitates or prevents movement, and especially dispersal movements, among habitat patches. Biotic connectivity is the degree to which the biotic landscape – composed of host(s), either static or mobile – facilitates or prevents movement, and especially dispersal movements, among habitat patches. Mobile hosts may have more or less complex movement trajectories resulting in contact probabilities with other hosts. Landscape conceptual models (adapted from (Sirami 2016) comprise 1) the 'patch–matrix' model (including 'island' and 'patch–corridor–matrix' models (Brudvig et al. 2017) and 2) the 'landscape mosaic' model. Red triangles correspond to focal patches. Black triangles correspond to individuals of the same species. Other black geometric forms correspond to individuals of other species. Arrows show movements.

of experimental designs, or have been performed in aquatic systems where connectivity is mostly driven by water connectedness (Liu et al. 2013, Dong et al. 2016).

### The particular case of biotic connectivity

In microorganisms associated with hosts, connectivity results from the relationships between a host and its microbiota (Fig. 1). Indeed, many microorganisms are associated with either animal or plant hosts, sometimes with a high degree of host-specificity (e.g. *Rhizobium leguminosarum*, which forms nodules with legumes). These different hosts may represent a set of ecological niches whose favorability depends on the degree of host-association: microorganisms can indeed be classified along a specialist–generalist gradient depending on the degree of host specialization. Microbial distribution is thus the result of a direct effect of host distribution that creates a biotic landscape, whose structure depends on the metapopulation dynamics of the hosts. Pathogen distribution patterns were modeled as depending on the composition and configuration of the biotic landscape (see for instance Holdenrieder 2004, Plantegenest et al. 2007, Meetemeyer et al. 2011 for reviews in landscape epidemiology) but not specifically at the microbial assemblage scale and depending on connectivity. Modelling connectivity in biotic landscapes is challenging. Connectivity may be ephemeral, depending on the probability of contact among hosts; or mobile, depending on the host’s ability to move across the landscape. Some approaches exist such as the Martensen et al. (2017)’s model that analyzes the dispersal of organisms as depending on spatial connectivity but also changes in habitat patches over time (i.e. the occurrence of ephemeral patches). Extending the spatio-temporal connectivity approach to microorganisms seems promising. This could be done by weighting the probability of temporal dispersal depending on the (possible) simultaneous existence of hosts – rather than of patches – between the time-steps considered.

## Mechanisms underlying connectivity effects

### Connectivity and dispersal

Increased landscape connectivity facilitates the dispersal of organisms among habitat patches (Wilson and Willis 1975, Beier and Noss 1998, Haddad et al. 2003, Gilbert-Norton et al. 2010; Fig. 2) thereby increasing population persistence and biodiversity (Wilson and Willis 1975, Haddad et al. 2017, Fletcher et al. 2018). The response of microorganisms to connectivity is likely to depend on their mode of dispersal. Microorganisms apply a wide range of dispersal strategies including frequent long-distance dispersal events, partly due to their ability to be dispersed by vectors such as water, wind or animals. The role of host movement in microbiota dispersal was recently quantified (e.g. passive mycorrhizal fungi transportation via birds (Correia et al. 2019); fungal spore dispersion by generalist

rodents (Stephens and Rowe 2020); transmission of microorganisms through seeds (Shade et al. 2017, Nelson et al. 2018)), which suggests that increased connectivity might promote the co-dispersal of microorganisms with their hosts. In addition, connectivity might influence passive dispersal for instance through wind (Avelino et al. 2012), droplets (Mukherjee et al. 2021), water flow (Dong et al. 2016) and marine currents such as for larval dispersal (Cowen and Sponaugle 2009) by modifying the intensity and direction of these vectors. However, there is also increasing evidence for very short dispersal distances via small vectors (e.g. earthworms or collembola in the case of soil microorganisms) (Feinstein and Blackwood 2013), active microorganism dispersion thanks to flagella in bacteria (Bashan 1986, Alexandre et al. 2004, Yang and van Elsas 2018), and multiplication of vegetative mycelium in soil fungi (Mony et al. 2021). Because motion and navigation capacity vary considerably among taxonomic groups and species (Bielčík et al. 2019), the effect of connectivity, and especially the scale of effect (Jackson and Fahrig 2012, 2015) (Box 1) may then depend to a great extent on the life-history traits of the microorganisms, such as the type of vector, body size and dispersal strategies. To give an example, the pathogen *Sclerotinia sclerotiorum*, has developed an astonishing trait, the synchrony of ejection of spores that is powerful enough to create a flow of air to facilitate dispersal of the spores (Roper et al. 2010).

In the case of habitat corridors, dispersal promotion (referred to as ‘dispersal effect’ in Fig. 2A) through increased connectivity can be correlated with other mechanisms that may also affect biodiversity responses. Indeed, corridors correspond to particular linear landscape elements that connect patches of similar habitat. Implementing corridors therefore contributes to an increase in both habitat area and edge amount; both processes that likely impact biodiversity (‘habitat amount’ and ‘edge’ effects; Fig. 2A). Disentangling the effect of corridors on dispersal from the indirect effect on habitat and edge amount has been investigated in macroorganisms (Brudvig et al. 2015, Haddad et al. 2017, Griffin and Haddad 2021). However, it remains an open question for microorganisms (Table 1; but see Sullivan et al. 2011, who compared the relative effect of the amount of edge and of dispersal on pathogens). Higher habitat amount (expressed as a larger patch) is assumed to increase carrying capacity and to result in a larger pool of species developing in the same habitat patch (MacArthur and Wilson 1967). In microbes, only a few studies tested and demonstrated such patch size effect on species richness (see for instance Peay et al. (2007) on ectomycorrhizal fungi). Also, corridors increase the amount of edges (i.e. boundaries between distinct types of patches (Ries et al. 2004); Fig. 2A). Corridor edges can facilitate species flux (i.e. boundary effects sensu Wiens et al. 1985). It particularly influences the arrival of organisms from the matrix (Fagan et al. 1999) including predator spillover (Fig. 2B). Edges also provide environmental heterogeneity that favors a larger number of organisms by modifying the local environmental conditions and providing unique niches (Fig. 2B). Only a few studies have quantified

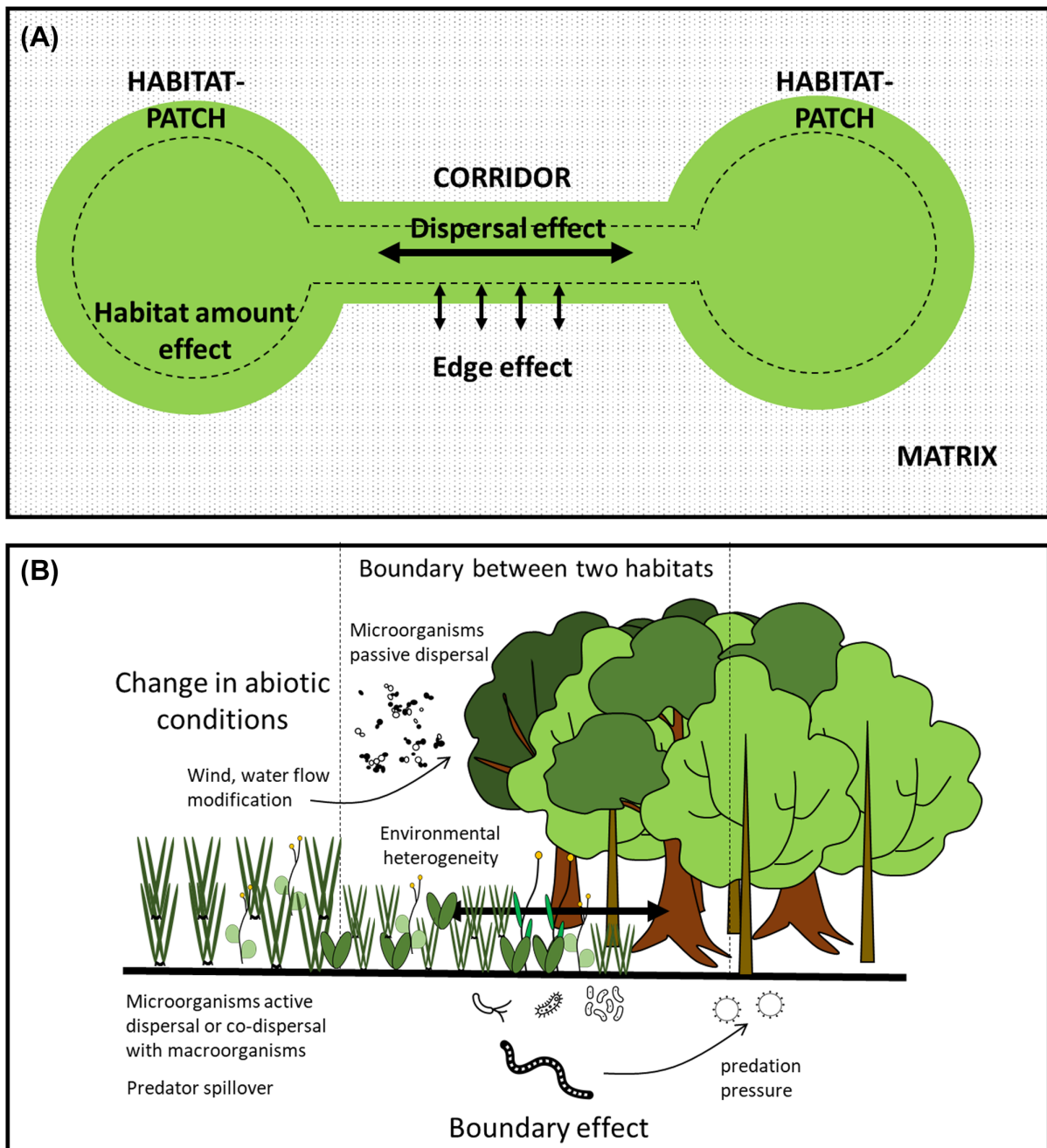


Figure 2. (A) Mechanisms underlying connectivity effects related to the particular case of corridors. The dispersal effect is linked to the movement of species from one habitat patch to another. The habitat amount effect increases the carrying capacity of patches, with large habitat patches and wide corridors increasing the total amount of habitat. The edge effect is linked to the influence of the interface on dispersal fluxes and abiotic conditions (see B). High edge amounts due to an increase of the perimeter of habitat patches and narrow corridors increase the influence of the boundary between habitats. (B) Focus on influences linked with the boundary zone between the corridor and the matrix (example of a forest corridor close to a matrix composed of grasslands). These influences include dispersal fluxes between the corridor and the matrix (spillover effect) and changes in abiotic conditions (new ecological niches at the interface).

the edge effect on microorganisms. Two studies conducted in several hundred meter long experimental corridors analyzed the effect of the presence and the shape of a corridor on microbes separately to control for the amount of edge. In these studies, edges either favored or hampered pathogen abundance (Sullivan et al. 2011 on four wind-dispersed and

splash-dispersed foliar fungi; Johnson and Haddad (2011) on a leaf fungal pathogen). These negative or positive edge effects were linked to two mechanisms: 1) a change in microclimatic conditions that affected the development of the fungal species and 2) a change in wind turbulence and hence in the spore deposition patterns within the habitat patch (Sullivan et al.

2011). The challenge is now to extend these results at the community level.

### **Host–microbe interactions as a strong mechanism of biotic connectivity**

In host-associated microorganisms, connectivity is related to host distribution in the landscape, and hence on host behavioral traits. Contrary to most macroorganisms, a key specificity of microorganisms is the existence of an interaction loop between hosts and the associated microorganisms: hosts provide niches or resources for microorganisms that in turn affect their meta-community dynamics (Miller et al. 2018). Microbiota often have a major effect on host performance via several ecological functions including nutrition, resistance to environmental and pathogenic stresses (for a review on plants, see Vannier et al. 2015). Pathogens may even cause the death of their host in the case of severe infection, while some microorganisms, such as protists, may also be preys for predator microorganisms. Beyond their direct effect on performance, some microorganisms also influence traits that modulate the probability of contacts among hosts. For instance, depending on the inoculum of fungi, a plant's clonal growth may be modified either through elongation and/or increased branching of stolons (for a review, see Bittebiere et al. 2020), thereby influencing the probability of transmission of fungi among plant ramets. In animals, some pathogens can also control the behavior of their hosts by influencing their social interactions and theretofore the transmission of the pathogen among individuals (see examples in the review by Klein 2003). Host–symbionts interactions have been integrated in the metacommunity conceptual framework (see introduction) in order to better understand how microbiota may shape host interactions within metacommunities (Mihaljevic 2012, Brown et al. 2020). The integration of the landscape in this framework is emerging. For instance, Miller and Bohannan (2019) demonstrated the effect of interactions among microbial dispersal traits and matrix permeability on the microbiota metacommunities associated with hosts. Further efforts should be made to include both direct and indirect effects of microorganisms on host distribution and movement, which might result in unique ecological processes that shape corridor–microorganisms relationships, especially through coadaptation.

### **Modeling connectivity in microorganisms: from biogeography to functional connectivity**

A wide range metrics have been developed (see Moilanen and Hanski 2001, Ricketts 2001, Moilanen and Nieminen 2002, Kindlmann and Burel 2008, Rayfield et al. 2011 for reviews) to quantify connectivity (or inversely, isolation) among habitat patches, either from a structural or a functional point of view (Tischendorf and Fahrig 2000, Calabrese and Fagan 2004, Taylor et al. 2006). Structural connectivity is rooted in the island biogeography (MacArthur and Wilson 1967) and

metapopulation theories (Levins 1970). It depends mainly on the physical attributes of the landscape elements. Measures typically focus on Euclidean distance between patches and/or on the size of the patches (e.g. the Euclidean distance to the nearest neighbor; probability of colonization of the model incidence function model (Hanski 1994a, b). Functional connectivity explicitly considers the response of organisms to the physical attributes of the landscape (Tischendorf and Fahrig 2000, Calabrese and Fagan 2004, Taylor et al. 2006). To this end, functional connectivity incorporates information on the potential or observed dispersal abilities of organisms within the matrix, such as differential permeability of the different habitat types in the landscape matrix. Closely related to the 'landscape mosaic' model, functional connectivity measures are assumed to better capture the preferential dispersal routes of organisms across the landscape matrix, as matrix heterogeneity is an important factor in determining organism dispersal (Ricketts 2001).

### **Structural connectivity**

Concerning microorganisms, a large proportion of studies that investigate the effect of connectivity on microorganisms focus on habitat isolation, the inverse of structural connectivity, using the Euclidean distance, assuming that the landscape matrix does not matter. These studies generally report the well-known distance-decay pattern predicted by the biogeography theory (see Clark et al. 2021 for a meta-analysis). For instance, Peay et al. (2010) used two types of metrics to test the effects of connectivity on fungal species richness on a single tree species, including distance to the mainland and distance to the nearest individual. The authors found that fungal species richness associated with *Pinus muricata* roots decreased when connectivity was measured as the distance to the mainland but was independent of the distance to the nearest individual, suggesting that species dispersal did not follow a stepping-stone connectivity model. To date, microbial studies conducted in the framework of the mosaic landscape model have only used a qualitative approach, in which connected and unconnected situations were compared (Ferrari et al. 2016). In that study, connected and disconnected situations were selected as two in-field configurations: vegetated patches that were continuous or separated by small circular mounds of soil formed by the action of frost and assumed to be barriers that isolated the sampling areas. The work demonstrated that the composition of the microbial assemblages in soil samples collected from the disconnected patches were more similar to each other but with fewer biological associations among species than connected areas. Like for macroorganisms, the assumption of an inhospitable matrix needs to be relaxed for microorganisms by considering the permeability of the different habitat types that make up the landscape matrix

### **Toward functional connectivity in microorganisms**

Functional connectivity metrics account for preferential dispersal routes across the landscape, reflecting more realistic dispersal distances (i.e. functional distances) among habitat



patches. This requires creating cost (or resistance) maps, in which cost (or resistance) values reflect the ecological cost of species moving through habitat and non-habitat patches of different kinds. As far as we know, only one microbial ecology study has been performed using functional connectivity metrics. Becker et al. (2017) analyzed the composition of the bacterial microbiota on amphibian skin of individual tree frogs located in forests that are connected to each other to varying extents. Forest connectivity was estimated from cost maps that classified forest habitats with a minimum cost (i.e. highly permeable) and other habitat types with a maximum cost (i.e. slightly permeable). The authors demonstrated that bacterial assemblages bore more resemblance to one another in better-connected patches, and that this was only significant when this functional metric was used instead of Euclidean distance. These findings suggest that more functional-based connectivity indexes are better predictors of movement of amphibians and of the dispersal of associated microbiota than geographical isolation alone. Such functional approaches might also be used for passive-dispersed microbes, by modeling matrix permeability differently depending on water current or wind flow. Transposing functional representations of the landscape developed for macroorganisms to microorganisms is a promising way to reach a more functional understanding of the corridor effect in this group. This requires a better description of the microorganisms' ecological niche both in terms of abiotic conditions and in the case of biotrophic organisms, of hosts and dispersal movement, to model resistance cost maps and preferential dispersal routes. Such mechanisms can be approximated by taking the life-history traits of the microorganisms into account. In addition, when the spatial extent at which landscape structure best predicts microorganism responses is lower than that typically envisioned for macroorganisms (see for instance the functional metrics used in Mony et al. (2020) for spatial extents of less than a meter), the use of functional connectivity metrics may be challenging as it requires a fine-grain resolution in the habitat maps. Recent advances in remote sensing methods might provide high resolution data for ecological applications (Sun et al. 2021) and be adapted to the particular case study of microorganisms.

## Impacts of connectivity on microbial populations and communities

### Effect on populations and communities

High connectivity is expected to promote population diversity and species richness by increasing genetic diversity and compensating for both population and community drift of isolated patches of habitat (Leibold et al. 2004). Nevertheless, high connectivity among patches and a high dispersal rate might also reduce species richness and population differentiation among patches by increasing the spread of individuals that are good competitors, parasites or pathogens (see Haddad et al. 2014 for a review). Yet, the effect of connectivity on microbial communities is assessed by looking

at a restricted number of parameters measured on populations or communities. For species-focused studies, population dynamics are measured through abundance (for instance spore counts) or through symptoms (for instance describing pathogen infection). For community studies, assemblages are described through composition or species richness, although the concept of species in microorganisms is still the subject of debate (Rosselló-Mora and Amann 2001, Konstantinidis et al. 2006, Novick and Doolittle 2021). In both situations, microbial population and community analyses have their intrinsic limits, as symptoms do not necessarily correspond to presence or abundance (i.e. asymptomatic individuals can be colonized by the species), and most current molecular analyses to describe microbial communities embed indistinctly both active and inactive microorganisms.

The great majority of studies of how connectivity affects microorganisms at the population scale concern pathogen dispersal (Plantegenest et al. 2007, Suzán et al. 2012 for reviews). Particular habitat patches, not necessarily of the same habitat type, have repeatedly been identified as ecological corridors for these pathogens. For instance, rivers were shown to disperse *Phytophthora alni* among alder trees through waterborne zoospores (Ioos et al. 2005). Roads have also been shown to be important corridors for pathogens due to dispersal caused by vehicle or foot traffic (Jules et al. 2002, Laine and Hanski 2006). More empirical evidence of the effect of connectivity more broadly than just corridors on microbial populations is needed. Future works should also consider species of other ecological guilds than pathogens, for instance mutualists, that have tremendous importance in ecosystem functioning, but also overlooked microorganisms with very low abundances. Such rare species represent the dominant part of microbial diversity (Nemergut et al. 2011) and are assumed to be key players in a number of biogeochemical processes and ecologic functions (Jousset et al. 2017).

Empirical evidence for the effects of connectivity on microbial communities has been provided by studies at the patch scale based on species richness or species composition, or at the metacommunity scale based on similarity among connected habitat patches. Response patterns to connectivity have been reported to be mixed. Positive effects of connectivity have been found for the transport of microorganisms in hydrological networks (Lindström and Bergström 2005) and on richness in ectomycorrhizal fungi (Peay et al. 2012). Increased similarity in fungal species composition in tree roots was found in connected patches compared to disconnected patches in a lava-fragmented landscape (Vannette et al. 2016). In contrast to these studies, others demonstrated the absence of relationships between microbial communities and connectivity. This absence was reported for arbuscular mycorrhizal fungi in sandy coastal plains in response to the distance to mainland environments (da Silva et al. 2017), or in assemblages associated with the roots of the herbaceous *Stachys sylvatica* growing in forest patches in response to the distance to the nearest forest stand (Boeraeve et al. 2019). The absence of impacts was hypothesized to be the consequence of a dominant effect of abiotic local factors on this taxonomic group.

Another explanation is that, depending on their biological traits, microorganisms respond to connectivity at a different spatial scale than macroorganisms. Shifts in the composition of the fungi in response to connectivity were shown to depend on fungal dispersal strategies (Vannette et al. 2016): species characterized by airborne spore dispersal were more abundant in isolated fragments, while fungi with poorly characterized dispersal or biotrophic lifestyle were more abundant in well-connected fragments. For microbes with low dispersal capacity, the connectivity effect could then occur at a much smaller spatial extent.

### Micro-connectivity for microorganisms

Spatial heterogeneity of microorganisms has been reported in many studies at a spatial grain size of a few centimeters (see for instance reviews by Franklin and Mills 2007, Bahram et al. 2015). Connectivity may thus be considerably downscaled, i.e. to less than 1 m<sup>2</sup> spatial extents as microbes may perceive environmental heterogeneity at a finer grain size than macroorganisms. At this extent, connectivity may affect microbial species distribution, and enable a mechanistic understanding that is impossible for macroorganisms.

Field observations provide some evidence for the existence of these micro-corridors. The first related studies analyzed the effect of connectivity on microbial assemblages. For instance, connectivity of soil pores, which represents discrete habitat patches, was shown to shape microbial communities. Bacteria dispersal depended on the mode of motility, pore size and matrix potential (Wolf et al. 2013). However, lower pore connectivity in soils increased microbial diversity (Carson et al. 2010). The authors explained this result by a sheltering effect of isolated particles from highly competitive organisms. In another study, connectivity among host plants, measured as a function of resistance distance among hosts, influenced endophytic fungal species richness (Mony et al. 2020), with a positive effect on richness for Basidiomycota, but a negative effect for Glomeromycota. The latter result was due to an increased edge effect.

Another set of studies reports that, through their development, individual organisms create a structural micro-corridor. This has been demonstrated for clonal plants. The clonal plant individual develops stolons along which microorganisms – bacteria and fungi – are transmitted (Vannier et al. 2018). More surprisingly, even within microorganisms, fungal hyphae have been shown to disperse bacteria while they are growing (Yang et al. 2017). This resulted from a continuous film of water developing along the hyphae that allowed motile microorganisms to swim (Kohlmeier et al. 2005). Because hyphae allow translocation of nutrients, as well as foraging for nutrient-rich patches or crossing nutrient-poor habitats (Boer et al. 2005), hyphal networks can be considered to guide a variety of soil microorganisms toward attractive nutrient-rich patches (Bravo et al. 2013). Communication among microorganisms that allows such active movement is an emerging research topic (Leach et al. 2017), and needs to be linked to the theoretical framework of corridor ecology.

Lastly, experimental micro-corridors have been used and tested on both fungi and bacteria. For instance, Rantalainen et al. (2004) set up microcosms of less than one m<sup>2</sup> in size to analyze the microbial colonization of sterile patches connected or not to a source patch (with a corridor). The presence of corridors did increase species richness in fungi, but only for some sampling time points in bacteria. The sometimes negative effect of corridors on bacteria was explained by increased competition for resources in the connected patches due to higher fungal species richness, suggesting microbial interactions are important at the patch level. Interactive effects between the corridor presence and the surrounding matrix were demonstrated by Spiesman et al. (2018), who analyzed the response of bacterial communities in connected and isolated patches of oak leaf litter in two types of matrix habitats (bare soil or pine litter). These authors found higher bacterial richness in isolated litter patches than in connected ones, and in patches surrounded by pine litter compared to bare soil, indicating a cross habitat spillover effect from the neighboring matrix (Box 1), probably of generalist species. In another experiment designed to test for the mechanisms underlying corridor effects, Rantalainen et al. (2005) investigated the role of enchytraeid worms as dispersal vectors in connected and unconnected systems. These authors showed that dispersal of saprophytic fungi in the corridors was promoted by the movement of these worms, and in the absence of worms, to a lesser extent, by vegetative growth. Studies on predator–prey dynamics also demonstrated the interactive effect of connectivity and species interactions on microorganism distributions (See for instance Holyoak 2000, Cooper et al. 2012), impacting ecosystem processes linked to microbial activity (Staddon et al. 2010). These experiments suggest the influence of small-scale connectivity on microbial community assembly, but also underline the importance of accounting for species interactions to understand the precise mechanisms of response to connectivity.

### Time-lagged responses to connectivity

In macroorganisms, especially if they are sessile, there is increasing evidence that assemblages do not respond to changes in connectivity instantaneously (Damschen et al. 2019, Lira et al. 2019). Time-lagged responses often occur because of the long lifespan of macroorganisms compared to the timespan of the study. They result from an extinction debt or a colonization credit (Box 1, Kuussaari et al. 2009 and Jackson and Sax 2010 for reviews on these concepts), following respectively, a loss or a gain in connectivity. Short-generation time of microbes suggests that these delayed responses are less likely, although a few authors have demonstrated time-lagged responses to connectivity in microorganisms.

Extinction debt was investigated and demonstrated in only one study. Berglund and Jonsson (2005) recorded a time lag in the decline in species richness of wood-inhabiting fungi in recently fragmented landscapes compared to old isolates. They observed a progressive decline in population densities

before complete disappearance of the species. Evidence for an extinction debt in bacteria has not been reported, but this phenomenon is likely. Indeed the ability of bacteria to remain dormant for long periods of time (Gray et al. 2019) enables long-term persistence of species even if the patch is isolated from other patches. Dormancy, which is a widely distributed trait in microorganisms influences species biogeographical patterns (Locey et al. 2020, Mestre and Höfer 2021) through its covariation with dispersal (Wisnoski et al. 2019).

Only one study reported, although incompletely, evidence for colonization credit in microorganisms. Peay et al. (2012) compared the composition of ectomycorrhizal fungi associated with the roots of oaks growing in old forest stands with that of fungi on the roots of oaks growing in recent stands, the recent stands being either isolated from or connected to old forests. Oaks in the recent stands had lower fungal species richness, suggesting a colonization credit, but the credit was even bigger in isolated stands than in connected ones, probably due to delayed dispersal in isolated stands. Some traits, such as dispersal capacity, might interact with the probability of colonization credit. Dormancy could also induce a delay in germination and slow down the colonization of habitats by new species.

Time-lagged responses of microbial assemblages are likely related to their dispersal strategies, such as short dispersal distances for colonization credit, and high vegetative multiplication and strong dormancy for extinction debt. In addition, while colonizing new patches, early-arriving species have a competitive advantage over later-arriving species ('priority effect' sensu Kennedy and Bruns 2005) and community composition may thus depend on historical variations in the order of arrival (Dickie et al. 2012). Analyzing the mechanisms underlying the time-lagged responses to connectivity also requires accounting for the key difference between microorganisms and macroorganisms: i.e. their very short generation time. For this reason, the effect of connectivity is likely to affect several generations of microorganisms with short dispersal distances, compared to the effect on macroorganisms whose dispersal movement occurs within the lifespan of the individual or within a few generations. In contrast to macroorganisms, microorganisms may be subject to evolutionary processes (e.g. adaptations mutations, and possibly even speciation) during their passage along the dispersal route especially if large spatial extents (i.e. hundreds of meters to kilometer) are considered. Genetic differentiation among microbial populations between donor and recipient patches could indeed occur because of the time it takes to pass through the dispersal route among patches. Consequently, one would expect detection of time-lagged responses to be challenging because depending on the species concept, species delimitation is coarse in prokaryotes.

## **Connectivity for the invisibles: from macroorganisms to microorganisms**

The extent to which connectivity is useful for a wide range of taxonomic groups is the subject of debate in many reviews

(Wilson and Willis 1975, Beier and Noss 1998, Murphy and Lovett-Doust 2004, Haddad and Tewksbury 2006, Gilbert-Norton et al. 2010, Haddad et al. 2011, 2015, Fletcher et al. 2016) although microbes are not included. Here we propose that the concept of connectivity is valid for microorganisms and emphasize that microorganisms respond to their landscape notably because of its influence on dispersal process. We also identified marked limitations and gaps in existing evidence on the topic (Table 1), pointing to a general need to acquire knowledge on microorganism reproduction and dispersal strategies, niche preferences and interactions with other groups. In the existing literature, we also identified major differences in the mechanisms and processes involved between microorganisms and macroorganisms. The main differences are 1) the spatial scale of the effect of corridors for some members of the microbial compartment. The spatial scale of effect could include much smaller spatial extents for microorganisms with short dispersal distance (active dispersal, dispersal through vegetative multiplication, or passive dispersal through vectors with short distance dispersal); 2) the temporal scale of effect, which might interact with the spatial scale of effect as it could include longer temporal scales in microbial responses, possibly involving evolutionary processes if the spatial scale considered is a few kilometers; shorter temporal scales might be considered for landscapes covering only a few square meters; 3) the use of unique dispersal pathways that represent 'biotic connectivity' provided by hosts. In such pathways, host-microbiota interactions are of primary importance and relationships with landscape structure may be shaped by a feedback effect of the microorganisms on the host distribution and dynamics. Biotic connectivity thus offers highly specific types of dispersal pathways.

Overall, this review has provided new insights into the rules governing microbial community assembly depending on connectivity and suggests new avenues for future research in the field (Table 1). Above all, in their current state, connectivity benefits macroorganisms and probably influences the section of the microbial community that disperses using macroorganisms as vectors. Corridors may also influence large-distance passive dispersal of microorganisms through the modification of wind or water fluxes (Damschen et al. 2014). However, the implementation of corridors, stepping-stones or highly permeable matrix must also be conceived at a finer spatial grain size to account for the diversity of lifestyles of microorganisms, and to address dispersal-limitation issues of the entire microbiota. Such fine-grained connectivity, especially the connectivity provided by hosts (i.e. biotic connectivity) could be established by preserving or even manipulating the arrangement of hosts in space, for example when planting species mixtures in crops. For free-living microbes, it could be insured by modifying the local heterogeneity in abiotic conditions at spatial scales of less than a meter, for instance through management practices, in order to establish areas that are more permeable for the dispersal of microorganisms. In the context of global change, microbial ecology will have to make the conservation of microbial diversity a priority in

future research owing the huge role of microorganisms in climate regulation, soil fertility, food and fiber production (Delgado-Baquerizo et al. 2016). A microbial rescue effect (Box 1; Mueller et al. 2020) promoted by microorganism-dedicated corridors at both small and large scales, could be envisaged. The need to expand ecological corridors for the ‘invisibles’ is thus timely.

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## Author contributions

**Cendrine Mony:** Conceptualization (lead); Writing – original draft (lead). **Léa Uroy:** Conceptualization (supporting); Writing – review and editing (lead). **Fadwa Khalfallah:** Writing – review and editing (supporting). **Nick Haddad:** Writing – review and editing (lead). **Philippe Vandenkoornhuys:** Conceptualization (supporting); Writing – review and editing (lead).

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