Heterogeneous dispersal networks to improve biodiversity science

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Opinion

Abstract

Dispersal plays a key role in shaping spatial patterns of biodiversity, yet its spatial heterogeneity is often overlooked in biodiversity analyses and management strategies. Properly parametrized heterogeneous dispersal networks capture the complex interplay between landscape structure and species-specific dispersal capacities. This heterogeneity, however, is recurrently neglected when studying the processes underlying biodiversity variation. To address this gap, we introduce a conceptual framework detailing the fundamental processes driving dispersal heterogeneity and its effects on biodiversity dynamics. We propose methods to parametrize heterogeneous dispersal networks, facilitating their integration into commonly used quantitative frameworks for biodiversity analyses. By considering the architecture of heterogeneous dispersal networks, we demonstrate their critical role in guiding biodiversity management strategies.

Keywords: Graph theory, Metacommunity, Spatial ecology, Ecological networks, Species movement

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Highlights

- Dispersal networks represent the spatial paths allowing individuals to move across landscapes, and model how dispersal shapes spatial patterns of biodiversity.

- Irregular patch arrangements and varying dispersal capacities among species generate heterogeneity in dispersal networks, which in turn affects α, β, and γ diversities.

- Spatial network structure should be considered explicitly in biodiversity analyses to assess the influence of dispersal.

- Empirical assessments of the influence of heterogeneity in dispersal networks on biodiversity variation can reveal dispersal limitation or, conversely, indicate a tendency for dispersal to homogenise communities.

- The architecture of dispersal networks can prove invaluable in guiding decisions on where and how to manage connectivity towards meeting biodiversity objectives within landscapes.

Dispersal is a heterogeneous process within spatial networks

Quantifying and understanding the factors driving spatial patterns of biodiversity is of critical importance in light of the continual reshuffling of biodiversity across space due to global environmental changes. Gaining a deeper understanding of the processes underlying spatial patterns of biodiversity becomes essential for managing landscapes and supporting biodiversity at multiple levels (α, β, and γ-diversities) and dimensions (taxonomic, functional, and evolutionary) [1, 2, 3, 4]. Ecological analyses and theories now recognise that both local coexistence mechanisms [5, 6, 7] and regional processes [8] are complementary and interact in determining complex spatial patterns of biodiversity [1]. The intricate interplay between local and regional processes stem from the diverse species responses to local environmental conditions, from interactions within and among species, and **dispersal** (see Glossary) dynamics [2, 9]. Since the emergence of **metapopulation** and **metacommunity** theories, dispersal has been acknowledged as a fundamental process driving biodiversity [1].

Modelling dispersal is inherently challenging, requiring ecologists and evolutionary biologists to rely on spatial networks and their associated assumptions to infer the influence of dispersal dynamics on biodiversity patterns. However, biodiversity analyses mostly rely on oversimplified representations of dispersal dynamics within landscapes. Simple **dispersal network** models, while advancing our understanding of the processes that shape biodiversity patterns, are critically impaired by implicit assumptions. For example, dispersal dynamics is often modelled as a simple function of geographic distances among pairs of patches (see Figure 1A for the simplest case of regularly arranged patches). These limitations hinder our capacity to adequately quantify the degree of isolation among individual patches, preventing simple dispersal networks from adequately capturing the inherent complexities of dispersal dynamics in biodiversity analyses.

Another inherent challenge is inferring dispersal dynamics by tracking individual movement across multiple species in space and time. While telemetry or genetic data are valuable, they may fall short in recovering complex dispersal dynamics [10-13]. Alternatively, these data can be employed to assist in parametrizing spatial quantitative frameworks to infer complex dispersal dynamics. One robust approach is to model the **dispersal paths** linking habitat patches using **graph theory** [14, 15]. In this framework, **dispersal networks** are depicted as **graphs** representing spatial relationships among local communities. Nodes correspond to habitat patches (e.g., islands, lakes, forests; habitat patches or simply patches are used interchangeably), and links correspond to potential dispersal paths, usually weighted by a function (e.g., exponential decay) of the spatial distances among patches (e.g., [16]). By integrating them into empirical biodiversity models, these networks are advancing biodiversity science, enabling us to analyse and quantify the influence of dispersal dynamics on biodiversity patterns [17, 18].

Dispersal networks, when properly parametrized, have a remarkable ability to capture and depict the spatially heterogeneous nature of dispersal dynamics within landscapes. **Dispersal heterogeneity** means that the dispersal behaviour of individuals, populations, or species is not constant over space within any given landscape, giving rise to diverse and **non-stationary** influences [19] on ecological processes and resulting biodiversity patterns. This heterogeneity arises from the interplay between two key components, namely structural and biological (or functional) [15, 20-22] (Figure 1). The structural component relates to the non-uniform and irregular distribution of habitat patches across the landscape [20]. Dispersal tends to be more prominent among patches that are geographically close. As such, it can be assumed that the physical component of dispersal networks is shared among species, irrespective of variations in

their **dispersal rates** and **dispersal capacities**. In contrast, the biological component encompasses variations in dispersal capacities among species, which exhibit significant heterogeneity in their propensity to disperse and abilities to successfully immigrate. For instance, when comparing two landscapes forming structurally similar dispersal networks (Figure 1A and 1C, or 1B and 1D), the biological component of dispersal heterogeneity (i.e., differing capacities of species to disperse) can lead to distinct biodiversity patterns, despite their similarity in patch distributions. The resulting interactions between structural and biological components lead to substantial heterogeneity in dispersal dynamics among local communities (Figure 1D) [15, 20].
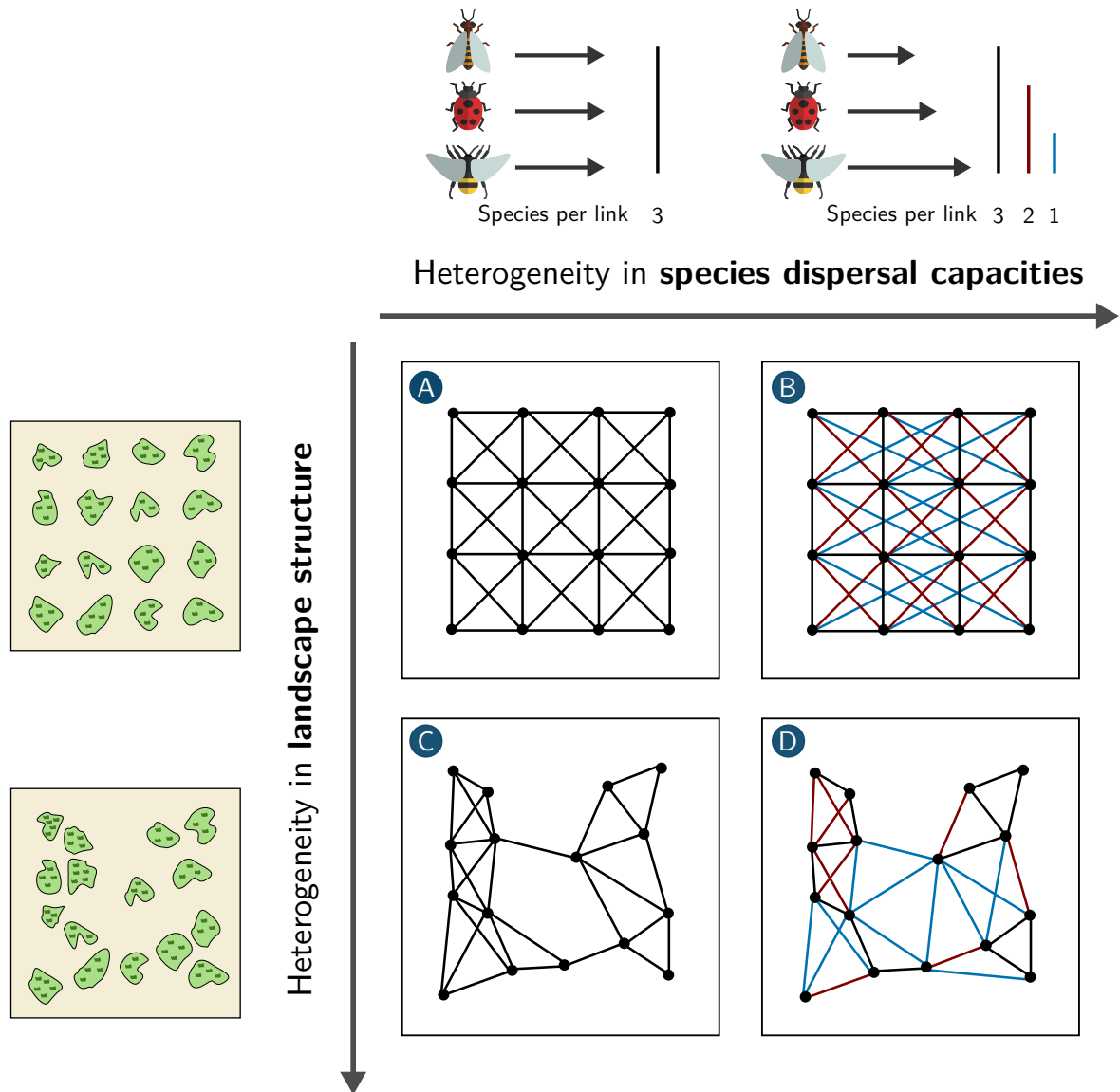
Figure 1: Dispersal network heterogeneity emerges from the interaction between landscape structure and species variations in dispersal capacities. Two factors interact to determine dispersal network heterogeneity: the irregularity of patch arrangements within landscapes and variations in species dispersal capacities. Vertical axis: from regular (A, B) to irregular (C, D) patch arrangements. On the left side, grassy habitat patches are represented in light green within a homogeneous landscape matrix (light brown). In the corresponding networks, the black dots represent the centroids of these habitat patches. Horizontal axis: from equal (A, C) to varying (B, D) species dispersal capacities. The length of the arrows is proportional to species dispersal distances. Link colours represent the number of species that can disperse through each path (ranging from 1 to 3). The shortest links can be covered by all three species (dark links), the longest by only one species (blue links), and the intermediate links by the two best dispersers (red links). The combination of these two structural and biological components (D) leads to heterogeneous dispersal networks with complex structures.

Heterogeneous dispersal networks underlie biodiversity variation

Heterogeneity in dispersal networks shapes biodiversity in metapopulations and metacommunities (Figure 2). Given that the time needed for a given species to spread across a network of patches depends on the interaction between structural and biological components, dispersal heterogeneity affects biodiversity dynamics [22-25]; and vice-versa. Assuming, for instance, that species are equivalent (i.e., neutral communities), the response of α diversity to dispersal rates depends on the **topology** of dispersal networks [16, 26]. Although α diversity is maximised at intermediate dispersal rates, these rates depend on how species can move along the links of dispersal networks. Even when dispersal capacities are assumed equal across species (for simplicity), the topology of heterogeneous dispersal networks supports higher levels of β-diversity than homogeneous ones (Figure 2C).

Heterogeneity in dispersal networks also affects biodiversity patterns when processes other than dispersal, including species responses to local environmental conditions and diverse types of biotic interactions, affect community compositions [27-29]. In landscapes characterised by contrasted environmental conditions across patches, **limited dispersal** hinders the ability of species to track their optimal environmental conditions [30-31]. Conversely, under competitive dynamics in less contrasted environments, when dispersal is not limited, the strongest competitors tend to dominate and homogenise local communities due to **mass effects**. Taken together, the structure of dispersal networks affects the dispersal rate at which a shift occurs between (i) a sub-optimal **environmental selection** limited by dispersal and (ii) a community homogenisation through dispersal (Figure 2) [32]. Thus, dispersal heterogeneity moderates the relative isolation of populations and communities, modulating environmental selection and species interactions.

Theoretical and empirical research show the influence of heterogeneous dispersal networks on biodiversity patterns (including our Figure 2). Single-species lab experiments conducted in micro- and mesocosms reproduced the theoretically expected effects of dispersal heterogeneity on population dynamics and spatial distributions [22-23, 33-34]. At the community level, riverine ecosystems have been the most studied and provide consistent empirical evidence for the effects of heterogeneous dispersal dynamics on biodiversity [35-39, see 27 for an example in another system]. Given the tree-like hierarchical nesting of streams within watersheds, they are prone to generating complex interactions between dispersal dynamics, local environmental conditions, and species interactions.

One challenge in inferring dispersal networks, regardless of their levels of heterogeneity, is the limitation of sampling designs to consider only a subset of habitat patches, often constrained by logistical limitations. Nevertheless, dispersal networks should encompass a more extensive range of patches (suitable and unsuitable), to accurately represent dispersal dynamics. Addressing this challenge can involve positioning each sampled patch within a more extensive dispersal network, achieved by leveraging information derived from land use maps and classified satellite imagery data. These data now make this habitat mapping possible in most cases, although mapping the diverse habitat preferences of generalist species may still prove challenging.
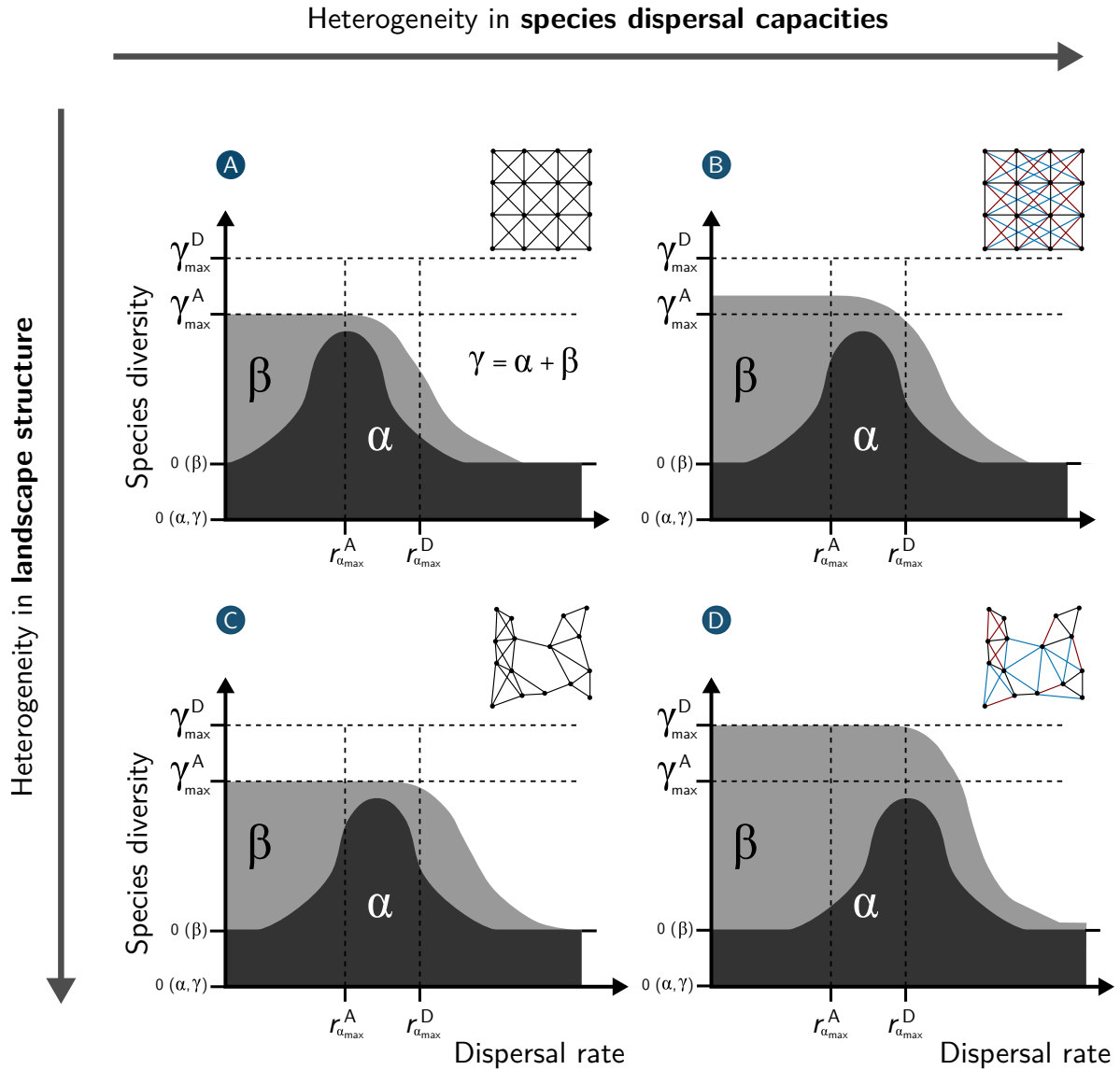
Figure 2: Dispersal heterogeneity underlies biodiversity variation. Hypothetical levels of α (dark grey area), β (light grey area), and γ diversities (sum of α and β, represented by the total dark and light grey area); and their hypothetical responses to increases in dispersal rates in homogeneous (A) and heterogeneous (B, C, D) dispersal networks. When dispersal rates increase, communities usually shift from being affected by dispersal limitation to maximising α diversity when species can optimally track resources. In the former case, communities eventually become homogenised when dispersal is not limited, and strong competitors tend to dominate. In a homogeneous dispersal network (A), α diversity is maximised at a dispersal rate $r^A_{\alpha_{max}}$, and the maximum γ diversity is γ^A_{max}.

When dispersal networks are heterogeneous due to either variations in dispersal capacities (B) or landscape structure (C), α diversity is maximised at a higher dispersal rate [12, 27]. When the two sources of heterogeneity interact (D), the dispersal rate is higher than expected from the combined (additive) effects observed in the cases B and C ($r^D_{\alpha_{max}}$). This interaction also leads to higher γ diversity (γ^D_{max} in case D) [24]. The red horizontal and vertical lines represent the maximum γ diversities (γ^A_{max}, γ^D_{max}) and the dispersal rate maximising α diversity ($r^A_{\alpha_{max}}$, $r^D_{\alpha_{max}}$), respectively, observed in the two extreme cases A and D. The networks on top of each plot are replicated from Figure 1 to illustrate further the effects of dispersal network heterogeneity in each case.

Building and integrating heterogeneous dispersal networks into biodiversity analyses

Within a single metacommunity, ecologists examine response and predictor variables at both the community level (α diversity) and the between-community level (β diversity). Despite the plethora of spatial methods used in biodiversity analyses, ecologists often fail to fully acknowledge their underlying assumptions about dispersal network characteristics. An example is the widely studied pattern of distance decay of similarity [40-41] that explores the spatial structure of β-diversity and community assembly by using complete pairwise geographic distance matrices derived from spatial coordinates of local communities. Complete distance matrices assume that all patches are connected, thereby missing the heterogeneity in dispersal dynamics due to dispersal barriers that cannot be traversed. Heterogeneity is also overlooked even when it is implicitly considered, such as in the commonly used **spatial eigenvectors** that involve the truncation of a geographic distance matrix [42]. This **truncation** process, seen as a simple analytical step, actually enhances the complexity of the spatial graph, allowing for the representation of some level of heterogeneity in dispersal networks.

Because different α and β diversity indices emphasize different ecological aspects (e.g., dominance, evenness, or simple taxonomic composition), one can contrast different hypotheses about dispersal heterogeneity and estimate which one(s) best fit(s) the ecological patterns and processes captured by these indices. These hypotheses can be contrasted by parametrizing dispersal networks with varying degrees of heterogeneity. These networks are designed to encompass both the structural and biological components of dispersal, and they can be informed or refined by incorporating prior knowledge and/or empirical data (e.g., telemetry, genetic data).

There are two main steps involved in modelling heterogeneous dispersal networks as spatial graphs: (i) modelling the topology of the network and (ii) modelling the strength of dispersal among interconnected local communities [42]. The first step identifies interconnected patches via dispersal, whereas the second involves determining variation in dispersal probabilities among patches for one or multiple species. Network topologies are represented by a pairwise matrix of connections between patches. They are usually depicted as an incomplete graph and its adjacency matrix, where connected pairs of communities (nodes) are represented by 1s (i.e., graph links), while zeros represent disconnected pairs (i.e., links removed after graph **pruning**). Usually, pairs of patches separated by geographic distances smaller than a given distance threshold remain connected (i.e., are given a value of 1). Threshold-based pruning can uncover the underlying structure of dispersal networks, including the spatial scales at which landscape structure imposes heterogeneities in dispersal networks [20, 43]. While a priori pruning removes links in dispersal networks based on hypotheses about dispersal heterogeneity, a posteriori pruning uses empirical data (e.g., telemetry or genetic data) to determine optimal topologies fitting the observed data. However, inferring the topology of dispersal networks from empirical data remains challenging and even if feasible, these topologies may not reflect well complex dispersal dynamics in space and time [10-12, 44-45].

The resulting topological matrix can be further refined by weighting the links among patches as distance functions (e.g., exponential) or dispersal probabilities. Dispersal probabilities can vary among species for a given link, which can also be assessed empirically from distributional data or by considering known dispersal capacities of species. Iterative processes such as simulating annealing and approximate Bayesian computation can be employed to test varying weights and assess which resulting heterogeneous networks maximise spatial patterns of α and β diversity. Although assigning very small weights to some links will be akin to pruning those links,

the consequences of such a weighting scheme for metrics purely based on the topology of the network differ. This renders essential the exploration of varying topologies to uncover all sources of spatial heterogeneity in dispersal and its consequences. Yet, manipulating both the structure and weights of topological matrices to represent dispersal probabilities remains computationally challenging [11], particularly considering the multiple ways in which species may vary in their dispersal capacities; and that the same species may vary in dispersal capacity across the landscape (a case not depicted in Figure 1 for simplicity). For instance, one may consider whether a single community-based, multiple single-species heterogeneous networks, or a consensus network based on the latter is more robust. Computing species-specific heterogeneous networks, for example, can estimate whether the influence of dispersal network heterogeneity arises mostly from landscape structure or from its interaction with varying dispersal capacities. Emerging multi-layer network approaches hold promise in combining multiple species-specific networks [46].

Once a heterogeneous dispersal network has been built, **centrality metrics** can explain variation among local communities in α diversity [36]. Similarly, **participation coefficients** can estimate the role of each patch in serving as hubs of dispersal between sub-networks of patches, or the spread of invasive species [20]. When analysing β diversity, the focal response variable becomes the compositional variation (turnover) among local communities. In this case, heterogeneous dispersal networks can be decomposed into spatial eigenvectors, employing techniques such as the widely used Moran's Eigenvector Maps [42]. The resulting eigenvector maps can then be used as predictors when empirically modelling variation in β biodiversity among local communities (as well as α diversity). Proposing different heterogeneous dispersal networks and their related eigenvector maps allows determining the levels of dispersal heterogeneity in the network that best fits with variation in α and β diversity.

At the regional scale, assessing the influence of different dispersal network structures on γ diversity is possible when data are available for multiple sets of metacommunities (or sub-metacommunities within a large one). In this case, various metrics describing the complexity or connectivity of heterogeneous networks can be used, including **modularity** indices [20, 43], algebraic connectivity [23] or other spectral properties of networks [14, 47]. Given the profound impact of the interplay between dispersal and habitat distribution on biodiversity at regional scales, we incorporate an exemplary case to demonstrate how dispersal network heterogeneity can contribute to resolving the long-lasting debate underlying SLOSS (Single Large vs Several Small) approaches to conservation (Box 1) [48-49]. The empirical test we propose (Box 1) also provides an estimate of the extent to which dispersal is limited within a landscape.

Box 1: Dispersal network heterogeneity provides new insights on the SLOSS debate

A long-lasting debate in ecology, called the SLOSS (Single Large vs Several Small) debate [48-49], revolves around the hypothesis that few large habitat patches can host more species than several smaller patches for the same total area. To test this hypothesis, two species accumulation curves are built to compare species richness per area unit between accumulated areas sampled in large-to-small and small-to-large patches. If the cumulative species richness increases more rapidly when the accumulated areas are sampled in several small patches, it suggests that these small patches include more species than large patches for the same total area (or vice-versa). Considering heterogeneity in dispersal networks could bring some consensus to this debate as it may act as a confounding factor in SLOSS analyses. Indeed, isolation and patch size may be correlated or not, depending on landscape structure and variation in species dispersal capacities. To consider dispersal heterogeneity in species accumulation curves, we introduce the SCSI (Several Connected versus Several Isolated patches) framework (Figure I). In this framework, species accumulation curves are built by adding patches starting either from the most connected patches and moving towards more isolated ones in the dispersal network (patches 30 to 1 on Figure IA), or vice-versa (see Figure IB and IC, respectively). When dispersal is limited, sampling an equal number of areas in well-connected patches should result in a higher number of species compared to the same number in isolated patches, regardless of patch sizes (Figure IB). Indeed, when species cannot effectively track suitable patches, the most connected patches in the dispersal network are expected to harbour a higher number of species. The area between the two curves estimates the strength of network heterogeneity influence on diversity patterns. If the accumulation curve drawn by adding patches from the most isolated to the most connected ones overlaps or stands above the reverse curve, it suggests that dispersal is not limited (Figure IC). In this case, dispersal heterogeneity plays a role in preventing isolated patches from being colonised solely by the strongest competitors. Note that varying levels of network heterogeneity can also be considered while estimating the optimal number of patches to preserve for maximising species richness at the landscape level. Our framework serves to (i) assess the influence of dispersal network heterogeneity on diversity patterns and (ii) distinguish between dispersal limitation and unrestricted dispersal. Its use could lead to a consensus in the SLOSS debate because the contribution to biodiversity of several small patches versus few large patches may depend on the complexity of the networks that connect them through dispersal.
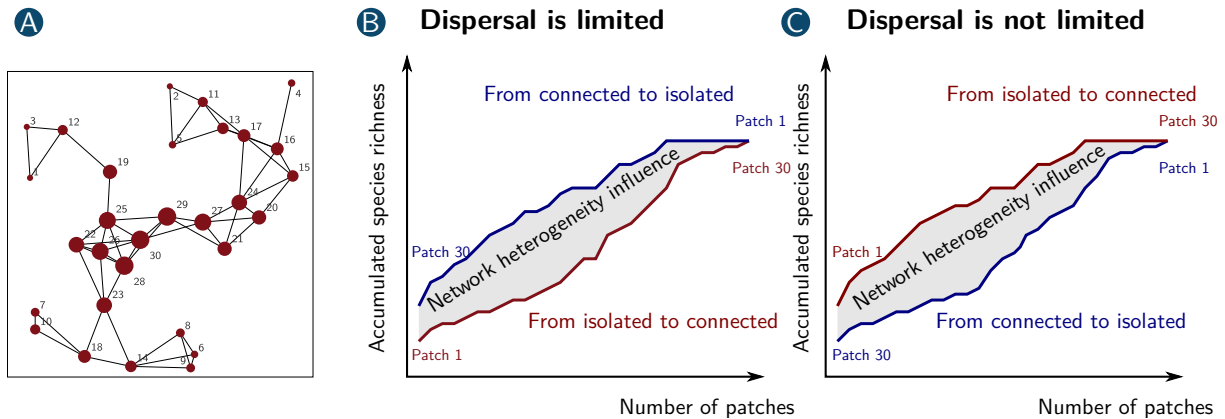
Figure I: A framework to empirically assess the effects of network heterogeneity on species diversity. A) Hypothetical heterogeneous dispersal network with 30 patches, exhaustively sampled to generate community data (i.e., species compositions at each patch). Numbers indicate the rank of each patch in terms of geographical centrality (closeness): largest values indicate patches that are the closest to all the other patches in average, (i.e., most connected), whereas lowest values indicate the most isolated patches. B) Dispersal is limited and prevents species from tracking optimal conditions through the network. For a given number of sampled patches, the accumulated species richness is higher when considering several well-connected patches than several isolated patches. C) Dispersal is not limited, leading the strongest competitors to dominate across most patches. In this case, the accumulated species richness should be higher when considering the most isolated patches, i.e., less reachable by the strongest competitors. In B) and C), the area between the curves represents the influence of dispersal network heterogeneity on diversity variation. These relationships are hypothetical and assume that equal areas are sampled within each sampled patch.

Heterogeneous dispersal networks for biodiversity management

The analysis of heterogeneous dispersal networks can guide biodiversity management strategies by optimizing connectivity management approaches aimed at identifying areas where spatial connectivity effectively supports long-term biodiversity conservation objectives [50-53]. More specifically, management strategies need to recognise that dispersal effects on biodiversity become increasingly scale and context-dependent when humans rewire dispersal networks by modifying habitats or introducing strongly competitive species [54]. Because of dispersal heterogeneity, the processes underlying biodiversity maintenance may vary among sets of spatial clusters of local communities that are, themselves, connected in varying degrees. As such, increases in dispersal rates can have both positive and negative effects on regional biodiversity. Clusters of habitat patches that exhibit stronger internal connections in contrast to connections with other sets of patches are referred to as modules in the graph theory literature [20]. These modules can serve as the basis for a relevant delineation of management area units for single species as they underly population synchronicity [52, 55] (Figure 3).

By building modules in which dispersal is more homogeneous and frequent, modularity offers potential solutions to address two common challenges faced by biodiversity managers. First, they assist in defining the spatial scale at which management efforts should be focused. Second, by aligning management strategies with the scale dictated by modularity, it is possible to make management strategies more context-dependent (Box 1 and Figure 3). Modules are, by design, sets that maximise the ratio between intra- and inter-module connectivity, allowing determining the patterns in species distributions that are due to dispersal heterogeneity. As such, if dispersal is limited, enhancing habitat connectivity among modules becomes critical to smooth the isolation gradient arising from network heterogeneity (Figures 2 and 3). Conversely, if dispersal is not limited and tends to homogenise communities by making most patches accessible (e.g., to strong competitors; Figures 2 and 3), then connectivity should be decreased via management. The module scale becomes then the most relevant scale for decision-making management strate-

gies. It should be noted that in this context, decreasing connectivity entails managing specific areas to disrupt dispersal flow for target species, while simultaneously providing habitats for other species that do not rely on the same dispersal networks.
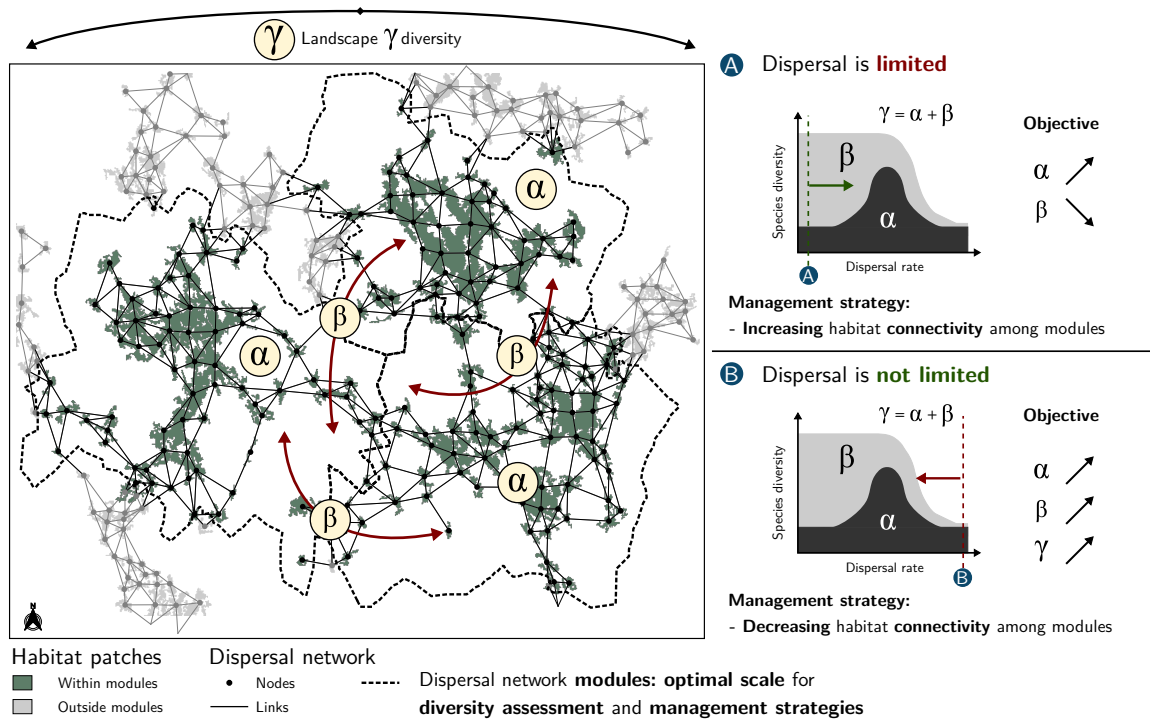
Figure 3: Analysing the modularity of heterogeneous dispersal networks to set the scale of management strategies maximising landscape γ diversity. The links of the dispersal network connect the centroids of forest habitat patches. Modularity analyses reveal three main modules at the center of the study area (cf. map legend). When dispersal is limited (A, right panel), a sensible conservation objective would consist in increasing habitat connectivity among modules to simultaneously increase module mean α diversity and decrease among module β diversity. This would allow dispersal limited specialist species to better track resources and colonise new patches within modules. When dispersal is not limited (B), decreasing connectivity among modules would allow less competitive species to locally dominate, thereby increasing all components of species diversity (α, β, γ). Habitat patches represent coniferous forest patches in the Laurentian Forest (Québec, Canada). Other smaller modules are not displayed for the sake of clarity. Spatial data source: Natural Resources Canada.

Concluding remarks

Dispersal networks are heterogeneous by nature as dispersal involves multiple species moving across heterogeneous landscapes. Dispersal heterogeneity has widespread effects on multiple levels and dimensions of biodiversity and sets the scale at which the strongest influences due to dispersal are relevant and observed. Considering the influence of network heterogeneity on biodiversity variation is key for understanding and predicting biodiversity dynamics and designing effective management strategies. However, our understanding of the complexity emerging from dispersal processes is hindered by numerous knowledge gaps (see Outstanding questions). Here, we focused on the potential interactions between landscape structure and dispersal capacities that lead to heterogeneous dispersal networks, and how we can study their influences on spatial variation in biodiversity. Although we have outlined and proposed methods to incorporate heterogeneous dispersal networks into biodiversity analyses, we urge for continued methodological advances in this area. Devising methods to accurately capture dispersal heterogeneity arising from the interactions between structural and biological components is also key in improving our ability to infer processes from patterns in ecology. These advancements can significantly benefit from the availability of recently accessible empirical dispersal data [13], alongside the use of telemetry, individual tracking, and genetic data.

Heterogeneous dispersal networks are expected to influence a wide range of biodiversity responses. The approaches covered here can be directly embedded into analyses of species abundance distributions [56-57], functional diversity patterns [36], and evolutionary processes [58], among others. Additionally, managers often face the challenge of designing optimal management strategies for multiple species that move through potentially semi-independent dispersal networks. Integrating dispersal heterogeneity into the complexity of decision-making requires practical solutions, and recent advances in multi-layer network approaches are promising in addressing further these methodological gaps [14, 46].

Acknowledgements

Declaration of interests

The authors declare no competing interests.

Outstanding questions

- How can we effectively disentangle the respective influences of landscape structure and species dispersal capacities on metacommunity diversity patterns, while taking into consideration the inherent heterogeneity in dispersal networks?

- At which spatial scale should we assess the influence of dispersal heterogeneity on biodiversity when species have different dispersal capacities? How can we parametrize (infer) dispersal network structure from empirical data?

- Can we enhance our capacity to predict the effects of land use change on biodiversity patterns by accounting species-specific impacts in dispersal network heterogeneity?

- Which graph-based methods most accurately capture the influence of dispersal heterogeneity on species diversity patterns? How can we enhance existing methods to make them more scale- and context-dependent?

- Can our Several Connected vs Several Isolated (SCSI) proposed empirical framework improve our understanding of the effects of dispersal on biodiversity? And can it help to resolve the long-standing debate surrounding the Single Large or Several Small (SLOSS) conservation strategies?

- How can we design optimal management strategies in landscapes where species exhibit varying levels of dispersal heterogeneity?

Glossary

Centrality metrics: quantitative measures for estimating the importance of a node given its position within a spatial graph. Includes degree, closeness, betweenness or eigenvector centrality indices, among other metrics.

Dispersal: movement of an individual or propagule from its natal patch to another patch, eventually followed by reproduction and gene flow.

Dispersal capacity: propensity and ability of individuals and propagules to disperse, determined by several life-history traits.

Dispersal heterogeneity: dispersal is spatially heterogeneous when the number of dispersing individuals varies among pairs of patches across the landscape, even when dispersal rates are constant.

Dispersal limitation: refers to the situation in which all species cannot reach all patches.

Dispersal network: spatial network formed by patches exchanging individuals and propagules, represented as a graph whose nodes are patches connected by spatial paths (links).

Dispersal path: spatial trajectory followed by individuals or propagules as they transition from their natal patch to another, where they possibly settle and reproduce.

Dispersal rate: fraction of individuals departing from a specific patch and potentially reproducing in another patch, irrespective of the distance covered during dispersal.

Environmental selection: process by which species composition of local communities is influenced by local environment.

Graph theory: field within combinatorial mathematics that focuses on the study of networks and their representation as graphs.

Heterogeneous dispersal network: heterogeneity in dispersal networks arise from the potential interaction between two components: the uneven distribution of patches within the landscape and differences in dispersal capacities among species.

Network/graph: a network is composed of interacting entities (e.g., here patches interacting via dispersal) and is commonly represented as a graph, which consists of discrete nodes connected by links.

Mass effects: situation in which dispersal is not limited, and a high influx of dispersers can override local competitive dominance.

Metacommunity: a set of local communities consisting of interacting species, which are connected through dispersal.

Metapopulation: set of local populations of a single species, which are connected through dispersal.

Modularity: graph's property where subsets of nodes are densely interconnected within each subset, with fewer connections to nodes outside. It serves as both an index to measure this pattern and a criterion for optimising the partitioning of graphs into modules.

Non-stationary: variation in the nature and intensity of a process (e.g., dispersal) over space (i.e., within a landscape). It is akin to spatial heterogeneity.

Participation coefficient: quantifies the level of connectivity of a node to other nodes across multiple modules. It identifies nodes that play an important role in promoting large-scale graph connectivity.

Patch: discrete spatial entity that supports a population or community and contains the necessary resources needed for species to fulfil their life cycle requirements. Individuals within and between species are assumed to interact, and population dynamics are assumed synchronous.

Topology: overall structure of connections within a network, which is typically represented by graph links. It describes the patterns of relationships and connectivity among nodes in a network.

Truncation/pruning: process of removing links from a graph. It involves eliminating specific connections between nodes, which can alter the structure and connectivity of the graph.

Spatial eigenvectors: set of orthonormal (i.e., orthogonal and linearly independent) vectors obtained through the diagonalisation of a quantitative matrix describing a spatial network. They are generally used as spatial predictors/covariates in general linear models or ordination frameworks for biodiversity analyses.

References

1. Leibold, M. A., and Chase, J. M. eds (2018) *Metacommunity ecology.* Princeton University Press.

2. Thompson, P. L. *et al.* (2020) A process-based metacommunity framework linking local and regional scale community ecology. *Ecol. Lett.*, 23, 1314-1329

3. Münkemüller, T. *et al.* (2020) Dos and don'ts when inferring assembly rules from diversity patterns. *Glob. Ecol. Biogeogr.*, 29 1212-1229

4. Pollock, L. J. *et al.* (2020) Protecting Biodiversity (in All Its Complexity): New Models and Methods. *Trends Ecol. Evol.*, 35, 1119-1128

5. Adler, P. B. *et al.* (2007) A niche for neutrality. *Ecol. Lett.*, 10, 95-104

6. Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.*, 31, 343-366

7. Letten, A. D. *et al.* (2017) Linking modern coexistence theory and contemporary niche theory. *Ecol. Monogr.*, 87, 161-177

8. Hubbell, S. P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography* (1st ed.). Princeton University Press

9. Leibold, M. A. *et al.* (2022) The internal structure of metacommunities. *Oikos.* e08618. DOI: 10.1111/oik.08618

10. Jacobson, B. and Peres-Neto, P. R. (2010) Quantifying and disentangling dispersal in metacommunities: how close have we come? How far is there to go? *Landsc. Ecol.*, 25, 495-507

11. Layeghifard, M. *et al.* (2015) Spatial and species compositional networks for inferring connectivity patterns in ecological communities. *Glob. Ecol. Biogeogr.*, 24, 718-727

12. Savary, P. *et al.* (2021) Analysing landscape effects on dispersal networks and gene flow with genetic graphs. *Mol. Ecol. Resour.*, 21, 1167-1185

13. Nathan, R. *et al.* (2022) Big-data approaches lead to an increased understanding of the ecology of animal movement. *Science*, 375. eabg1780. DOI:10.1126/science.abg1780

14. Dale, M. R., and Fortin, M. J. (2021) *Quantitative analysis of ecological networks.* Cambridge University Press.

15. Fortin, M. J. *et al.* (2021). Network ecology in dynamic landscapes. *Proc. Roy. Soc. B*, 288, 20201889

16. Economo, E. P. and Keitt, T. H. (2008) Species diversity in neutral metacommunities: a network approach. *Ecol. Lett.*, 11, 52-62

17. Clappe, S. *et al.* (2018) Beyond neutrality: Disentangling the effects of species sorting and spurious correlations in community analysis. *Ecology*, 99, 1737-1747

18. Windsor, F. M. *et al.* (2023) Using ecological networks to answer questions in global biogeography and ecology. *J. Biogeogr.*, 50, 57-69

19. Rollinson, C. R. *et al.* (2021). Working across space and time: nonstationarity in ecological research and application. *Front. Ecol. Environ.*, 19, 66-72

20. Gilarranz, L. J. (2020). Generic emergence of modularity in spatial networks. *Sci. Rep.*, 10, 1-8

21. Henriques-Silva, R. *et al.* (2015) On the evolution of dispersal via heterogeneity in spatial connectivity. *Proc. Roy. Soc. B*, 282. 20142879

22. Rayfield, B. *et al.* (2023) Spread of networked populations is determined by the interplay between dispersal behavior and habitat configuration. *Proc. Natl Acad. Sci. U.S.A.*, 120. e2201553120. DOI: 10.1073/pnas.2201553120

23. Arancibia, P. A. and Morin, P. J. (2022) Network topology and patch connectivity affect dynamics in experimental and model metapopulations. *J. Anim. Ecol.*, 91, 496-505

24. Gilarranz, L. J. *et al.* (2017) Effects of network modularity on the spread of perturbation impact in experimental metapopulations. *Science*, 357, 199-201

25. Holland, M. D. and Hastings, A. (2008) Strong effect of dispersal network structure on ecological dynamics. *Nature*, 456, 792-794

26. Economo, E. P. and Keitt, T. H. (2010) Network isolation and local diversity in neutral metacommunities. *Oikos*, 119, 1355-1363.

27. Bode, M. *et al.* (2011) Different dispersal abilities allow reef fish to coexist. *Proc. Natl Acad. Sci. U.S.A.*, 108, 16317-16321

28. Gilarranz, L. J. *et al.* (2015). Hot Spots of Mutualistic Networks. *J. Anim. Ecol.*, 84, 407-13

29. Zhang, H. *et al.* (2021) Dispersal network heterogeneity promotes species coexistence in hierarchical competitive communities. *Ecol. Lett.*, 24, 50-59

30. Abrahms, B. *et al.* (2021) Emerging Perspectives on Resource Tracking and Animal Movement Ecology. *Trends Ecol. Evol.*, 36, 308-320.

31. Schlägel, U. E. *et al.* (2020) Movement-mediated community assembly and coexistence. *Biol. Rev.*, 95, 1073-1096

32. Suzuki, Y. and Economo, E. P. (2021) From species sorting to mass effects: spatial network structure mediates the shift between metacommunity archetypes. *Ecography*, 44, 715-726

33. Cunillera-Montcusí, D. *et al.* (2021) Metacommunity resilience against simulated gradients of wildfire: disturbance intensity and species dispersal ability determine landscape recover capacity. *Ecography*, 44, 1022-1034

34. Thompson, P. L. *et al.* (2017) Loss of habitat and connectivity erodes species diversity, ecosystem functioning, and stability in metacommunity networks. *Ecography*, 40, 98-108

35. Altermatt, F. and Fronhofer, E. A. (2018) Dispersal in dendritic networks: Ecological consequences on the spatial distribution of population densities. *Freshw. Biol.*, 63, 22-32

36. Borthagaray, A. I. *et al.* (2020) Community isolation drives lower fish biomass and species richness, but higher functional evenness, in a river metacommunity. *Freshw. Biol.*, 65, 2081-2095

37. Larsen, S. *et al.* (2021) The geography of metapopulation synchrony in dendritic river networks. *Ecol. Lett.*, 24, 791-801

38. Lee, F. *et al.* (2022) Network topology mediates freshwater fish metacommunity response to loss of connectivity. *Ecosphere*, 13. e4286. DOI: 10.1002/ecs2.4286

39. Tonkin, J. D. *et al.* (2018) The role of dispersal in river network metacommunities: Patterns, processes, and pathways. *Freshw. Biol.*, 63, 141-163

40. Graco-Roza, C. *et al.* (2022) Distance decay 2.0 - a global synthesis of taxonomic and functional turnover in ecological communities. *Glob. Ecol. Biogeogr.*, 31, 1399-1421

41. Martínez-Santalla, S. *et al.* (2022) Assessing the nonlinear decay of community similarity: Permutation and site-block resampling significance tests. *J. Biogeogr.*, 49, 968-978

42. Dray, S. *et al.* (2006) Spatial modelling: A comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecol. Modell.*, 196, 483-493

43. Borthagaray, A. I. *et al.* (2014) Modularity along organism dispersal gradients challenges a prevailing view of abrupt transitions in animal landscape perception. *Ecography*, 37, 564-571

44. Keitt, T. H. *et al.* (1997) Detecting critical scales in fragmented landscapes. *Conserv. Ecol.*, 1, 1-17

45. Gilarranz, L. J. *et al.* (2015) Inferring topology from dynamics in spatial networks. *Theor. Ecol.*, 8, 15-21

46. Bianconi, G. (2018). *Multilayer Networks: Structure and Function.* Oxford University Press.

47. Shanafelt, D. W. *et al.* (2017) Do-it-yourself networks : A novel method of generating weighted networks. *R. Soc. Open Sci.*, 4, 171227

48. Fahrig, L. *et al.* (2022) Resolving the sloss dilemma for biodiversity conservation: a research agenda. *Biol. Rev.*, 97, 99-114

49. Riva, F. and Fahrig, L. (2022) The disproportionately high value of small patches for biodiversity conservation. *Conserv. Lett.*, 15. e12881. DOI: 10.1111/conl.12881

50. Brennan, A. *et al.* (2022) Functional connectivity of the world's protected areas. *Science*, 376, 1101-1104

51. Chase, J. M. *et al.* (2020) Ecosystem decay exacerbates biodiversity loss with habitat loss. *Nature*, 584, 238-243

52. Gonzalez, A. *et al.* (2017) Spatial ecological networks: planning for sustainability in the long-term. *Curr. Opin. Environ. Sustain.*, 29, 187-197

53. Schiesari, L. *et al.* (2019) Towards an applied metaecology. *Perspect. Ecol. Conserv.*, 17, 172-181

54. Bullock, J. M. *et al.* (2018) Human-mediated dispersal and the rewiring of spatial networks. *Trends Ecol. Evol.*, 33, 958-970

55. Foltête, J.-C. and Vuidel, G. (2017) Using landscape graphs to delineate ecologically functional areas. *Landsc. Ecol.*, 32, 249-263

56. Koffel, T. *et al.* (2022) A general framework for species-abundance distributions: Linking traits and dispersal to explain commonness and rarity. *Ecol. Lett.*, 25, 2359-2371

57. McGlinn, D. J. *et al.* (2019) Measurement of Biodiversity (MoB): A method to separate the scale-dependent effects of species abundance distribution, density, and aggregation on diversity change. *Methods Ecol. Evol.*, 10, 258-269

58. Boussange, V. and Pellissier, L. (2022) Eco-evolutionary model on spatial graphs reveals how habitat structure affects phenotypic differentiation. *Commun. Biol.*, 5, 1-12