Spatial networks of habitats, populations, and communities: connecting approaches to keep cutting edges

Savary, Paul*[1]

[1] *Université Marie et Louis Pasteur, CNRS, ThéMA, 32 rue Mégevand F-25000 Besançon, France*

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Abstract

Purpose of review: Spatial networks are extensively used in ecology to represent exchanges among landscape features (e.g., habitat patches, river segments) or biological entities (e.g., individuals, populations, communities). I reviewed the literature produced in the past 25 years using these networks. Distinct types of spatial networks have emerged in several subfields of ecology. I aimed to assess whether this gave rise to disconnected research silos or, in contrast, whether methodological similarities generated bridges to connect theoretical frameworks.

Recent findings: I reviewed 679 papers using eight types of spatial networks. Habitat networks were the most used, usually for connectivity assessments with conservation-oriented purposes. In contrast, studies using metapopulation, metacommunity, or river networks were the most embedded in theoretical ecology. Population genetic networks were essentially used in landscape genetics, whereas dispersal networks and spatial networks found more diverse uses. Finally, meta-networks combining several of the above have more recently favored the integration of these typically disconnected approaches.

Summary: The lack of connection among research branches mobilizing spatial networks mainly stems from an opposition between applied and theoretical objectives, further reinforced by the differentiation of journal scopes. This divergence can create a mismatch between recent theoretical advances and current methodological designs, possibly affecting the tested predictions and result interpretations. Yet, the diversity of spatial networks is also beneficial. Provided it is acknowledged properly, future works could advantageously build upon existing frameworks for cutting-edge research, as exemplified by recent works on meta-networks.

Keywords: spatial networks, graph theory, dispersal, connectivity, gene flow, rivers

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[*] Corresponding author: `paul.savary@umlp.fr`

1 Introduction

What happens when species move is one of the most important questions in ecology, and one that is of particular interest to spatial ecologists [1]. Exchanges among populations, communities and the habitats they occupy partly explain population synchrony, gene flow, or colonization-extinction dynamics and, consequently, the diversity and distribution of species over space and time. Increasingly, spatial ecologists have worked towards breaking down the drivers and influences of these spatial interactions by making use of network theory. The potential of network-based approaches for ecological research has grown steadily in the past decades and given rise to a wide range of flexible methods [28, 108]. Among the tools now available, spatial networks are networks whose components (nodes and links) have spatial coordinates and can be represented on a map [28]. They differ from interaction networks (e.g., aspatial food webs or pollination networks) by the fact that one needs to define nodes and links from the spatial location of existing landscape features or biological entities, often assigning weights to their components (e.g., node areas or abundance, link (cost)-distances) rather than using binary incidence matrices [29]. A spatial network (or graph) represents the internal dynamics of populations, communities, or habitat patches (nodes) connected by movements that are constrained by the topology and connectivity of network links.

Several branches of spatial ecology adopted spatial networks in the early 2000s with different motivations, approaches, and theoretical backgrounds. Landscape ecologists have long been interested in the influence of habitat patch distribution, matrix resistance, and corridors on ecological processes shaping biodiversity patterns. This emphasis on landscape structure and a research agenda closely linked to biodiversity conservation found in spatial networks an efficient way to model habitat connectivity. As illustrated by Urban & Keitt (2001)[134], habitat patch networks can be represented by "landscape graphs" or "patch-based graphs" in which nodes and links are defined from landscape features, respectively habitat patches and the potential movement paths among them (Figure 1, Box 1). Similarly, freshwater ecologists have used spatial networks to represent the dendritic structure of riverine ecosystems [5, 19, 20], with links matching the hydrographic network and diverse types of nodes (populations, communities). Alongside these rather structural networks, spatial networks have represented networks of biological entities connected by species movements in spatially-explicit translations of the metapopulation theory [66], metacommunity theory [37], or population genetic models [34] (Figure 1, Box 1). These approaches came with their own mathematical tools (e.g., conditional independence graphs [34]) but also generated specific ecological predictions (e.g., relationship between network diameter and the $\frac{\alpha}{\beta}$ diversity ratio [37]). Later, the integration of some of these approaches led to "meta-networks" of varying natures.

This diversity can be seen as a strength for the use of spatial networks in ecology. Their adoption in several research branches has created conditions for continuous innovations and parallel enrichment, as seen in other fields of ecology. For instance, a review by Wainwright et al. [138] showed that restoration ecology studies have recently increased their references to community ecology to better align restoration practice with community assembly mechanisms. Whether applied works making use of spatial networks have increasingly mobilized their theoretical counterparts remains to be assessed. Indeed, it is equally likely that the use of spatial networks in distinct research branches has led to disconnected research silos despite their methodological similarities. The recent divergence of the theoretical ecology and conservation biology literatures is an example of such a trend [68]. The specialization of scientific journals and a narrow reading of the very abundant literature can create echo chambers specific to each subfield and further disconnect them over time [42, 126]. Accordingly, assessing whether the flourishing literature on spatial networks has given rise to research silos or to fruitful exchanges is crucial. On the one hand, it could determine whether there are opportunities for new frameworks combining existing approaches and whether methodological innovations align with recent theoretical advances. On the other hand, it could identify examples of successful integrations, and thereby, a way forward.

I conducted a literature review of the use of spatial networks in ecology over the past 25 years. I compared the publication trends (volume, journals, keywords) and cited references of research works using distinct types of spatial networks to quantify their relative integration or disconnection. I then described the specific and shared characteristics of the identified research branches, and discussed the potential consequences of their current level of integration. I end this review with recommendations and potential next steps, building on new and existing approaches within and outside the surveyed fields.

Box 1: Spatial networks in ecology

Spatial networks usually fall into the following categories, differing by the structural or biological nature of their nodes and links (Figure 1):

Defined from structural landscape features:

Habitat networks: Their nodes correspond to discrete habitat patches and their links to potential movement paths (e.g., dispersal or migration movements) [134]. They are referred to as "habitat (patch) networks", "landscape graphs", or "patch-based graphs" [56], among others. These networks are commonly used to assess habitat connectivity, compute and visualize corridors or connectivity metrics, prioritize conservation measures, or estimate impacts. Software programs used to build these networks include Conefor Sensinode [118] and Graphab [47].

River networks: Their links correspond to river branches, making them dendritic networks (i.e., tree-like), whereas their nodes are most often river junctions or river segments. These nodes can be directly associated with populations or communities. These networks often serve as a basis to investigate metapopulation or metacommunity dynamics or the respective influence of community assembly processes in riverine ecosystems [19, 20, 44].

Defined from biological entities:

Population genetic networks: Their nodes correspond to populations or individuals of the same species, while their links are estimated from their pairwise genetic differentiation or other proxies of gene flow (e.g., landscape distances, group assignment probabilities). They are used to describe population genetic structure and investigate landscape genetic relationships, as initially proposed by Dyer & Nason with the "popgraph" approach [34].

Metapopulation networks: Their nodes are populations subject to extinction-colonization dynamics and their links describe the dispersal connections among such populations. These networks are a graph-based representation of spatially-explicit metapopulations, as conceptualized by the seminal work of Ilka Hanski and collaborators [62, 64]. They can serve as a basis to (i) estimate the parameters of metapopulation models (e.g., incidence, colonization, or extinction local functions, metapopulation extinction time or capacity) or (ii) to simulate metapopulation dynamics in varying network structures.

Metacommunity networks: Their nodes are communities whereas their links represent potential dispersal paths giving rise to metacommunity dynamics, i.e., a combination of species sorting, biotic interactions, and dispersal movements shaping diversity patterns at landscape scale. The works of Economo & Keitt [37, 36] set the ground for the use of this approach; see [122] for a recent synthesis.

Meta-networks: These networks are made from a combination of at least one spatial network and another network, spatial or not, linked in an explicit way to the former. They include networks in which a species interaction network (e.g., food web, pollination network) is embedded within each spatial node, spatial networks connected to other networks representing human infrastructures or discrete time steps, spatial networks having different types of nodes and links (e.g., habitat or movement types) or connections to aspatial entities (e.g., species) (Figure 4).

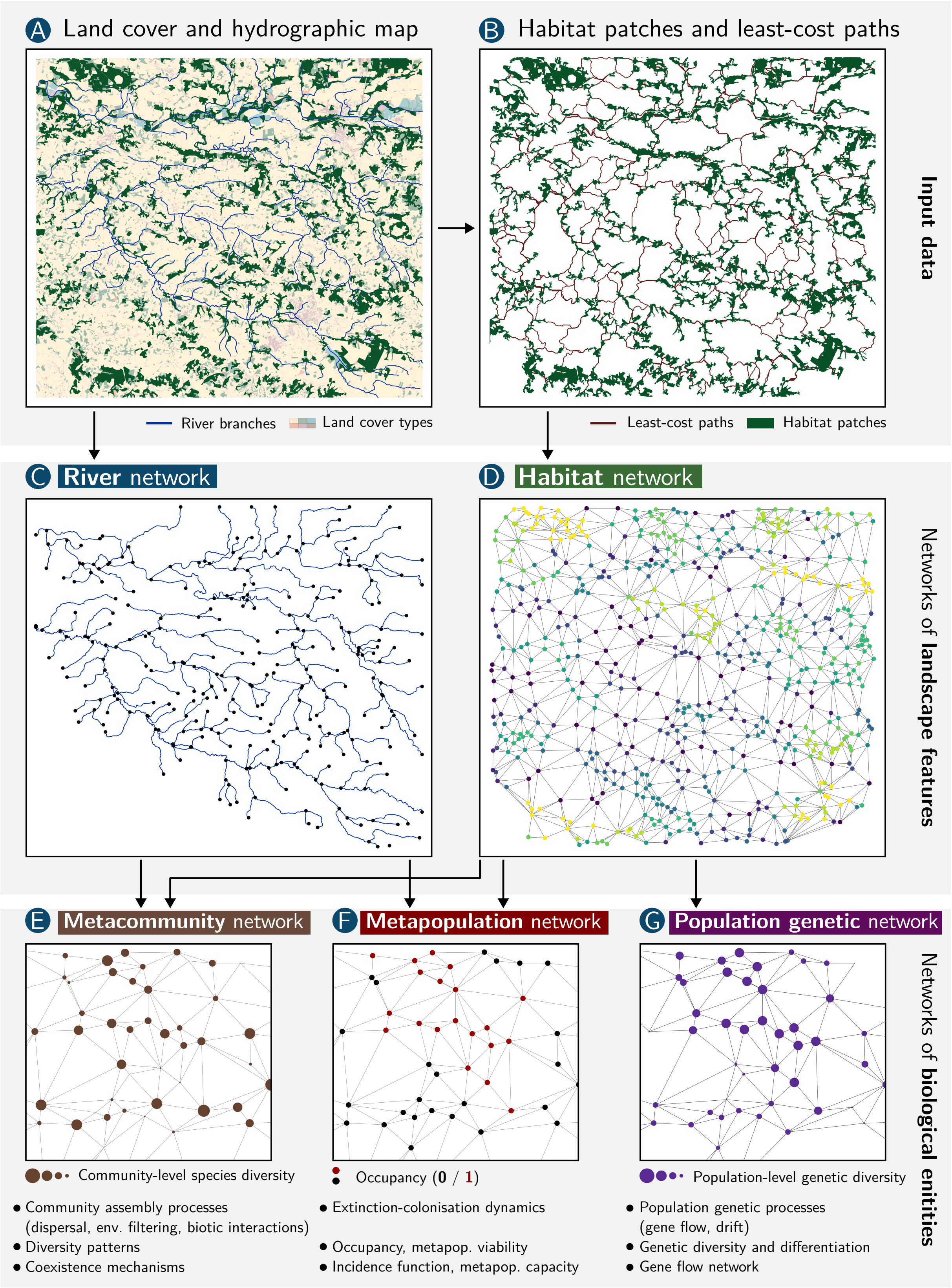

Figure 1: Spatial networks used in ecology and considered in this review. (A) Input data used to build spatial networks often include data on landscape features such as land cover and hydrographic map. (B) Habitat patches and least-cost paths (and corresponding cost-distances) computed for building habitat networks. (C) Dendritic river network built from the hydrographic map. Nodes represent river junctions and links river branches. (D) Habitat network built from forest patches (nodes) and least-cost paths (links). The Flux metric has been computed at the node-level; blue to yellow circles represent low to high values, respectively. (E, F, G) Metacommunity, metapopulation, and population genetic networks representing networks of biological entities used for studying different processes, patterns, and mechanisms, as listed below. Circle size and color represent community-level species diversity (brown circles), binary occupancy status (red: occupied, black: vacant), and population-level genetic diversity (purple circles). The construction of population genetic networks from river networks was less frequent and is not represented here. The study area (500 km^2) considered for making the figure is centered on 43°40'N; 0°43'W (South-Western France). See details in the Supplementary Information.

2 Search and analysis of publications about spatial networks

I searched for scientific publications about "spatial networks" first published between 2000 and 2024 using a Web of Science query. To be retrieved, the publications had to include in their thematic fields a combination of terms related to (i) the nature of the graphs/networks, (ii) the processes under investigation, and (iii) the scientific fields they originate from. I used a query of the form '`(i) AND (ii) AND (iii)`' (see full query in Supplementary Information). The first part of the query (i) targeted the nature of the networks, using combinations of the following terms: graphs/networks of habitats, patches, (meta)populations, or (meta)communities; genetic, spatial, landscape, or dispersal graphs/networks; graph/network-based indices or metrics; Conefor or Graphab software programs. At least one combination of these terms had to be present (e.g., "habitat graph" or "metapopulation network"). They were separated by the logical word OR. The second part of the query (ii) targeted the processes under investigation with the terms: "connectivity", "movement", "dispersal", "colonization", "migration", "gene flow", "range expansion", or "range shift". The third part of the query (iii) targeted the scientific field with the terms: "ecology", "evolution", "conservation", "landscape genetics", "population genetics", and "biodiversity". This broad query initially identified 1260 publications. I then excluded publications from journals outside the field of ecology, evolution, and conservation biology. I inspected manually every publication to assign them a type of spatial network. This allowed me to exclude works that were not relevant to the present review, as some works included the above-mentioned terms but did not actually build or analyse spatial networks, nor review their use. The final corpus included 679 articles from 131 scientific journals, later referred to as papers or studies.

The network types assigned to each paper to define 8 research branches were the following: habitat networks, river networks, metapopulation networks, metacommunity networks, population genetic networks, dispersal networks, spatial networks, and meta-networks. Studies using metapopulation networks were distinguished from other studies about metapopulations by the explicit use of the term "network" when describing the methods or interpreting the metapopulation dynamics (e.g., effect of network structure on survival). Population networks and community networks were considered as metapopulation or metacommunity networks, respectively, when used alongside references to the corresponding theory. The criteria used to distinguish the spatial networks are summarized in Box 1. Two broad reviews about network use in ecology were considered separately [12, 28].

I extracted the full list of references cited in the main text of the papers, as well as the keywords provided by the authors. I identified the most frequent journals, cited references, and keywords for each spatial network type, and qualitatively described the most common or original research approaches within each research branch. During the manual inspection, experimental studies were identified, as well as other characteristics of the studies such as the type of ecosystems or habitats investigated or the composition of the meta-networks. I finally assessed the rate of citation across all research branches of the most frequently cited references in each branch and of key references introducing theories or software tools (see full list in the Supplementary Information). All the codes used for the initial analysis and the final annotated corpus are available online (see Data Availability Statement). The publication search was performed in June 2025. I analysed citations and keywords with the package `bibliometrix` [9] in R [110]. Finally, I performed population genetic and metacommunity simulations for Box 2; whose methods are detailed in the Supplementary Information.

3 Publication trends

The 679 papers of the corpus included 313 studies about habitat networks (Figure 2A). The second most frequent network type was metapopulation networks ($n = 128$), followed by meta-networks ($n = 82$), population genetic networks ($n = 60$), river networks ($n = 34$), and metacommunity networks ($n = 33$). Dispersal networks ($n = 21$) and spatial networks ($n = 6$) were less represented, and used in studies on very diverse topics such as invasion biology, spatial epidemiology, or pest management. Papers using the latter networks are not described in as much details as the others, for the sake of brevity.

The annual number of papers about spatial networks increased from 2000 to 2024, although it tended to stabilize after 2012 for most types of spatial networks (Figure 2B). The trend was then sustained by an increase in the number of studies using meta-networks. Habitat networks have mostly been used after 2010. This can be explained by their initial development in the early 2000s [134, 135], followed by user-friendly software programs and guidelines for metric use around 2010 [47, 91, 112, 118]. The number of papers about metapopulation networks stayed relatively constant over the whole period because the metapopulation theory was introduced in the late 1990s [66, 63, 64] and continuously updated since then. The use of population genetic networks was relatively constant after the publication of the "popgraph" approach [34] in 2004, coinciding with the early stages of landscape genetics as a field [85]. The use of metacommunity networks and river networks began after 2006, following key publications about dendritic riverine ecosystems [44, 20], metacommunity theory [80], and the use of networks to investigate these systems [5, 37, 38].

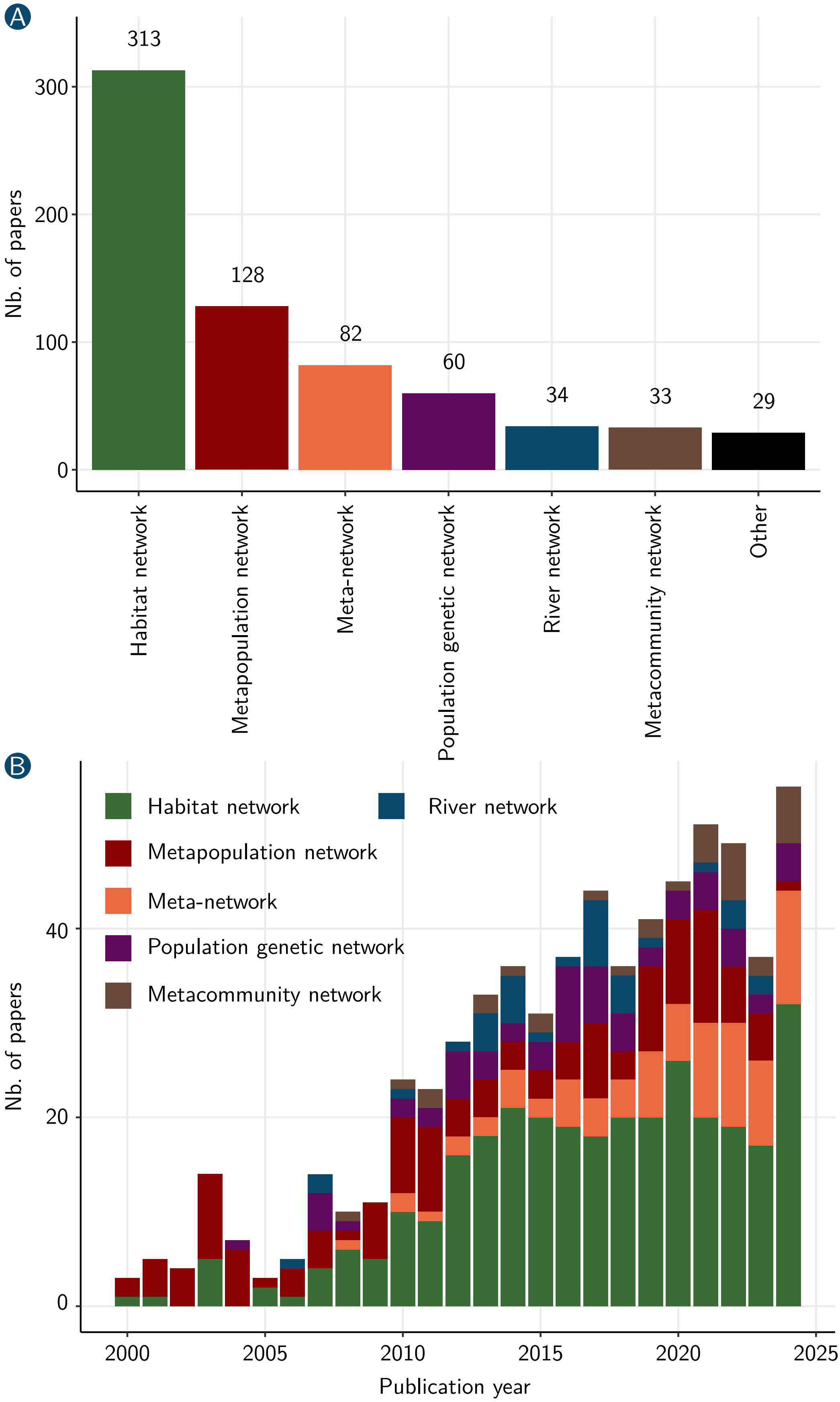

Figure 2: Total (A) and annual (B) number of papers published from 2000 to 2024 using each type of spatial networks considered in this review ($n = 679$). See Box 1 for a description of the spatial networks. The category "Other" includes dispersal networks, spatial networks, and two reviews about networks in ecology.

4 Differentiation in publication sources, cited references, and keywords

The studies using distinct spatial networks formed research branches differing substantially in the journals publishing them (Figure 3), the keywords used by authors to define their work (Table 1), and the content and scope of their cited references (Table 2). 29 journals out of 131 published more than 6 studies using spatial networks (Figure 3), and 4 of them published more than 25 papers: Landscape Ecology (63), Ecological Indicators (37), Ecological Modelling (34), and Biological Conservation (28). While 47 % of the papers published in Ecological Modelling were about metapopulation networks, the vast majority of papers in Ecological Indicators, Landscape Ecology, and Biological Conservation were about habitat networks (92 %, 83 %, 57 %, respectively). Beyond these examples, the proportion of papers about habitat networks published in each journal revealed a gradient ranging from journals with applied to methodological and theoretical scopes (Figure 3B). Habitat networks were dominant in journals of applied ecology (e.g., Landscape and Urban Planning, Ecological Indicators, Journal of Environmental Management) or conservation biology (Table 1). In contrast, these networks were almost absent in specialized journals where meta-networks, metapopulation networks, or population genetic networks dominated (Movement ecology, Journal of Theoretical Biology, Molecular Ecology, respectively). More generalist ecology journals published all approaches relatively equally (The American Naturalist, Oikos, Ecology Letters, Journal of Animal Ecology, Ecography).

As reflected by author keywords (Table 1), studies using habitat networks often mobilized graph theory to assess connectivity and habitat fragmentation, and predict dispersal in generically called "ecological networks". The presence of "Circuit theory" in their most frequent keywords and 17 publications in Ecological Modelling or Methods in Ecology & Evolution stress the emphasis of these studies on the methods. In contrast, papers using metapopulation, metacommunity, or population genetic networks stressed the biological entities (metapopulation, metacommunity), processes (dispersal, extinction, colonization, gene flow, community assembly), and common patterns under study (metapopulation dynamics, biodiversity, genetic diversity, genetic structure, isolation by distance). Studies using river networks shared similarities with studies using metacommunity networks in terms of publications sources (e.g., Ecology Letters, Oikos) and keywords (metacommunity, dispersal). They were referring more frequently to their biological models (e.g., Chinook salmon, fish passage) and 5 of them were published in the specialized journal Freshwater Biology. Similarly, 18 studies using population genetic networks were published in Molecular Ecology, Conservation Genetics, and Molecular Ecology Resources. Finally, the keywords of studies using meta-networks were general terms associated with network-based analyses of metacommunity, connectivity, and dispersal.

The references cited in papers using each type of spatial network pointed to another source of differentiation among corresponding research branches: their theoretical and methodological background (Tables 2 and 3). The seminal paper by Urban & Keitt [134] introducing the habitat network approach was cited in 46 % of the studies using these networks. Similarly, they often cited the works of Santiago Saura and collaborators, which introduced commonly used graph-based connectivity metrics [100, 116, 117] and the Conefor software [118]. In the 10 most cited references of this research branch, the paper by Taylor et al. [130], introducing the concept of landscape connectivity, is the only non-methodological reference.

The most cited references in studies about metapopulation networks were the publications setting the ground of metapopulation theory (e.g., [66, 64, 81]). Studies using population genetic networks cited classical population genetic references (e.g., [143]), applications of the method (e.g., [57]), and references to common population genetic tools such as genetic distances or clustering methods [43, 107, 140]. This is due to the use of genetic networks in complement to other population genetic methods in the same studies. Papers about river networks frequently referred to theoretical and empirical works on the dynamics and diversity of riverine ecosystems [21, 20, 44], and to the seminal paper of Leibold et al. [80] about metacommunities. Finally, papers on meta-networks borrowed

Table 1: 10 most frequent journals publishing research on spatial networks and 10 most frequent keywords used by their authors, for each research branch using a distinct type of spatial network. The columns '# (%)' include the number of times a journal published a paper about a type of spatial network, and between brackets, the corresponding proportion of papers of that branch published in this journal; or the number of times a keyword was mentioned in papers about a type of network, and the proportion of papers of that branch mentioning this keyword. Sometimes, less than 10 journals published more than 1 paper using a spatial network type, hence the blank fields.

Network type	**Most frequent journals**	**# (%)**	**Most frequent keywords**	**# (%)**
Habitat network n = 313	Landscape Ecology	52 (17)	Graph theory	68 (22)
	Ecological Indicators	34 (11)	Connectivity	53 (17)
	Landscape and Urban Planning	17 (5)	Landscape connectivity	48 (15)
	Biological Conservation	16 (5)	Fragmentation	25 (8)
	Journal of Applied Ecology	11 (4)	Dispersal	23 (7)
	Ecological Modelling	9 (3)	Habitat fragmentation	22 (7)
	Conservation Biology	8 (3)	Circuit theory	20 (6)
	Methods in Ecology and Evolution	8 (3)	Functional connectivity	19 (6)
	Ecological Applications	7 (2)	Habitat connectivity	19 (6)
	Journal of Environmental Management	7 (2)	Ecological networks	18 (6)
Metapopulation network n = 128	Ecological Modelling	16 (13)	Metapopulation	34 (27)
	Ecology	9 (7)	Connectivity	17 (13)
	Ecography	8 (6)	Dispersal	13 (10)
	Biological Conservation	7 (5)	Habitat fragmentation	13 (10)
	Ecological Applications	6 (5)	Extinction	10 (8)
	Oikos	5 (4)	Metapopulation dynamics	10 (8)
	The American Naturalist	4 (3)	Habitat network	9 (7)
	Biodiversity and Conservation	4 (3)	Habitat quality	7 (5)
	Journal of Animal Ecology	4 (3)	Colonization	6 (5)
	Journal of Theoretical Biology	4 (3)	Fragmentation	6 (5)
Meta-network n = 82	Movement Ecology	6 (7)	Spatial networks	14 (17)
	Ecological Modelling	5 (6)	Metacommunity	9 (11)
	Ecological Applications	4 (5)	Network	9 (11)
	Journal of Animal Ecology	4 (5)	Connectivity	7 (9)
	Methods in Ecology and Evolution	4 (5)	Graph theory	6 (7)
	The American Naturalist	3 (4)	Network analysis	6 (7)
	Ecology	3 (4)	Ecological networks	5 (6)
	Ecology Letters	3 (4)	Dispersal	4 (5)
	Molecular Ecology	3 (4)	Habitat connectivity	4 (5)
	Proc.Roy.Soc.B	3 (4)	Modularity	4 (5)
Population genetic network n = 60	Molecular Ecology	14 (23)	Landscape genetics	13 (22)
	PLoS ONE	5 (8)	Gene flow	11 (18)
	Ecology and Evolution	4 (7)	Graph theory	11 (18)
	Journal of Biogeography	3 (5)	Dispersal	9 (15)
	Biological Conservation	2 (3)	Genetic structure	7 (12)
	Conservation Genetics	2 (3)	Genetic connectivity	5 (8)
	Landscape Ecology	2 (3)	Genetic diversity	5 (8)
	Methods in Ecology and Evolution	2 (3)	Genetic network	5 (8)
	Molecular Ecology Resources	2 (3)	Connectivity	4 (7)
	Proc.Roy.Soc.B	2 (3)	Isolation by distance	4 (7)
Metacommunity network n = 33	Ecography	5 (15)	Metacommunity	9 (27)
	Ecology Letters	4 (12)	Dispersal	7 (21)
	Frontiers In Ecology and Evolution	3 (9)	Biodiversity	6 (18)
	Oikos	3 (9)	Metacommunities	3 (9)
	Global Change Biology	2 (6)	Metapopulation	3 (9)
	Scientific Reports	2 (6)	Neutral theory	3 (9)
			Centrality	2 (6)
			Community assembly	2 (6)
			Connectivity	2 (6)
			Landscape perception	2 (6)
River networks n = 34	Freshwater Biology	5 (15)	Dispersal	9 (26)
	Journal of Applied Ecology	4 (12)	Connectivity	8 (24)
	Ecological Applications	3 (9)	Graph theory	5 (15)
	Ecology Letters	2 (6)	Metacommunity	4 (12)
	Landscape Ecology	2 (6)	Chinook salmon	2 (6)
	Molecular Ecology	2 (6)	Conservation planning	2 (6)
	Oikos	2 (6)	Dendritic ecological network	2 (6)
	PNAS	2 (6)	Dendritic networks	2 (6)
			Fish passage	2 (6)
			Gammarus fossarum	2 (6)

methods and ideas from a broad literature. Although mentions to Urban & Keitt's approach [134] and to Leibold et al.'s metacommunity framework [80] were frequent, these studies also referred to tools dedicated to the analysis of several types of networks (`igraph` [27], `bipartite` [32]), and to empirical applications of species interaction networks [13, 97].

Overall, the most cited references in papers using a specific network type were rarely cited in papers using a different spatial network (Table 3). For instance, the methodological reference by Saura & Pascual-Hortal [116] was cited in 23.3 % of the papers, but in 44.4 % of those about habitat networks, 12.2 % of papers about meta-networks, and in less than 10 % of the other papers. Similarly, papers about population genetic networks frequently cited references that are rarely cited in studies about other networks (e.g., [34, 57, 85]). In contrast, the references by Hanski & Ovaskainen [65] and by Levins [81] about metapopulations are frequently cited in studies about river and metacommunity networks. Some general references are cited relatively equally across branches (Table 3), such as the review by Dale & Fortin about spatial networks [28], the presentation of the `igraph` R package [27], or the review by Fahrig [46] about the effect of habitat amount and fragmentation on biodiversity; all cited by more than 5 % of the papers of almost all branches despite their low overall citation rate. The divergence of research branches exhibited by the rates of citation of these key references was visible on the result of a correspondence analysis of Table 3 included in the Supplementary Information.

Finally, key references of theoretical ecology were mostly cited in papers about metacommunity networks, river networks, or meta-networks. This is the case of the article by Chesson [23] about coexistence mechanisms and by Mouquet & Loreau [94] about source-sink metacommunities, both exclusively cited in the latter research branches (Table 3). Although habitat networks were sometimes used to predict the effect of habitat connectivity on species diversity based on patterns of habitat area and isolation, only 2.2 % of the papers using these networks cite the book of MacArthur & Wilson [84] about island biogeography theory. Similarly, while such predictions are often made under implicitly neutral assumptions, the book about the neutral theory of biodiversity by Hubbell [70] was not cited in any paper about habitat networks, but in 33 % and 12 % of the papers about metacommunity or river networks, respectively.

Table 2: 10 most cited references in papers about each spatial network type. The column 'Nb.citations (%)' includes the number of citations of the reference in the corresponding research branch using a type of spatial network, as well as the proportion of publications of that branch citing this reference.

Network type	Most cited references	Nb.citations (%)
Habitat network n = 313	Urban & Keitt, 2001. *Ecology*	145 (46)
	Saura & Pascual-Hortal, 2007, *Landscape and Urban Planning*	139 (44)
	Pascual-Hortal & Saura, 2006, *Landscape Ecology*	99 (32)
	Saura & Torné, 2009, *Environmental Modelling & Software*	94 (30)
	Saura & Rubio, 2010, *Ecography*	90 (29)
	Urban et al., 2009, *Ecology Letters*	89 (28)
	Taylor et al., 1993, *Oikos*	86 (27)
	Galpern et al., 2011, *Biological Conservation*	75 (24)
	Calabrese & Fagan, 2004, *Front. Ecology Environ.*	74 (24)
	McRae et al., 2008, *Ecology*	68 (22)
Metapopulation network n = 128	Hanski, 1994. *Journal of Animal Ecology*	42 (33)
	Hanski, 1999. *Metapopulation Ecology*	40 (31)
	Hanski, 1998. *Nature*	31 (24)
	Hanski & Ovaskainen, 2000. *Nature*	29 (23)
	Levins, 1969. *Bulletin of the Entomological Society of America*	24 (19)
	Hanski et al., 1994. *Ecology*	17 (13)
	Moilanen & Nieminen, 2002. *Ecology*	17 (13)
	Brown & Kodric-Brown, 1977. *Ecology*	16 (13)
	Hanski et al., 1996. *Conservation Biology*	15 (12)
	Hanski et al., 2000. *Ecology*	15 (12)
Meta-network n = 82	Urban & Keitt, 2001. *Ecology*	18 (22)
	Csardi & Nepusz, 2006. *InterJournal*	16 (20)
	Olesen et al., 2007. *PNAS*	12 (15)
	Dale & Fortin, 2010. *Annual Reviews Ecol. Evol. System.*	10 (12)
	Guimerà & Nunes Amaral, 2005. *Nature*	10 (12)
	Leibold et al., 2004. *Ecology Letters*	10 (12)
	Saura & Pascual-Hortal, 2007, *Landscape and Urban Planning*	10 (12)
	Bascompte et al., 2003. *PNAS*	9 (11)
	Dormann et al., 2008. *The R Journal*	9 (11)
	Pilosof et al., 2017. *Nature Ecology & Evolution*	9 (11)
Population genetic network n = 60	Dyer & Nason, 2004. *Molecular Ecology*	42 (70)
	Dyer et al., 2010. *Molecular Ecology*	22 (37)
	Garroway et al., 2008. *Evolutionary Applications*	21 (35)
	Weir & Cockerham, 1984. *Evolution*	18 (30)
	Wright, 1943. *Genetics*	18 (30)
	Pritchard et al., 2000. *Genetics*	17 (28)
	Urban & Keitt, 2001. *Ecology*	15 (25)
	Excoffier et al., 1992. *Genetics*	13 (22)
	McRae, 2006. *Evolution*	13 (22)
	Rozenfeld et al., 2008. *PNAS*	13 (22)
Metacommunity network n = 33	Leibold et al., 2004. *Ecology Letters*	23 (70)
	Hubbell, 2001. *The Unified Neutral Theory of Biodiv. and Biogeo.*	11 (33)
	Urban & Keitt, 2001. *Ecology*	11 (33)
	Mouquet & Loreau, 2003. *The American Naturalist*	9 (27)
	Carrara et al., 2012. *PNAS*	7 (21)
	De Bie et al., 2012. *Ecology Letters*	7 (21)
	Economo & Keitt, 2008. *Ecology Letters*	7 (21)
	Economo & Keitt, 2010. *Oikos*	7 (21)
	Logue et al., 2011. *Trends in Ecology & Evolution*	7 (21)
	Mouquet & Loreau, 2002. *The American Naturalist*	7 (21)
River networks n = 34	Fagan. 2002. *Ecology*	17 (50)
	Campbell Grant et al., 2007. *Ecology Letters*	15 (44)
	Carrara et al., 2012. *PNAS*	13 (38)
	Altermatt, 2013. *Aquatic Ecology*	12 (35)
	Brown & Swan, 2010. *Journal of Animal Ecology*	11 (32)
	Carrara et al., 2014. *The American Naturalist*	11 (32)
	Leibold et al., 2004. *Ecology Letters*	11 (32)
	Muneepeerakul et al., 2008. *Nature*	11 (32)
	Peterson et al., 2013. *Ecology Letters*	11 (32)
	Vannote et al., 1980. *Canadian J. of Fish. and Aquat. Sci.*	8 (24)

Table 3: Proportion of citations of the most cited or key theoretical or methodological references in papers about each spatial network type. The references are ordered in decreasing order of their citation rate in the whole corpus (column "Overall"). Values are displayed in bold when a reference is more frequently cited in a specific research branch than it is in the whole corpus.

Cited reference	Overall	Habitat networks	Metapopulation networks	Population genetic networks	Metacommunity networks	River networks	Meta-network
Urban et Keitt, 2001. *Ecology*	32.0	**46.3**	8.6	25.0	**33.3**	17.6	22.0
Saura & Pascual-Hortal, 2007, *Land.Urb.Plan.*	23.3	**44.4**	1.6	5.0	3.0	8.8	12.2
Urban et al., 2009, *Ecology Letters*	18.1	**28.4**	4.7	8.3	**18.2**	14.7	9.8
Taylor et al., 1993, *Oikos*	16.3	**27.5**	5.5	11.7	6.1	2.9	8.5
Saura & Torné, 2009, *Environ.Model.Soft.*	16.2	**30.0**	0.8	10.0	3.0	5.9	4.9
Galpern et al., 2011, *Biological Conservation*	14.4	**24.0**	0.8	13.3	6.1	11.8	7.3
McRae et al., 2008, *Ecology*	13.0	**21.7**	1.6	**18.3**	3.0	2.9	3.7
Calabrese & Fagan, 2004, *Front. Ecology Environ.*	12.8	**23.6**	2.3	1.7	3.0	8.8	3.7
Adriaensen et al. 2003. *Land.Urb.Plan.*	11.6	**21.4**	3.1	8.3	0.0	2.9	2.4
Rayfield et al. 2011. *Ecology*	11.3	**18.9**	0.8	8.3	6.1	2.9	9.8
Hanski, 1998. *Nature*	10.3	6.1	**24.2**	6.7	9.1	8.8	9.8
Hanski & Ovaskainen, 2000. *Nature*	10.0	6.7	**22.7**	3.3	**12.1**	**11.8**	7.3
Fahrig, 2003. *Annual Reviews EES*	9.9	**14.4**	6.3	5.0	9.1	0.0	8.5
Hanski, 1994. *Journal of Animal Ecology*	9.9	5.8	**32.8**	0.0	6.1	8.8	1.2
Dale & Fortin, 2010. *Annual Reviews EES*	9.0	**9.9**	3.1	8.3	**12.1**	**11.8**	**12.2**
Levins, 1969. *Bull.Entomo.Soc.Am.*	8.5	4.8	**18.8**	3.3	**18.2**	**8.8**	**8.5**
Hanski, 1999. *Metapopulation Ecology*	8.2	3.5	**31.3**	0.0	3.0	2.9	1.2
Leibold et al., 2004. *Ecology Letters*	8.1	1.3	4.7	0.0	**69.7**	**32.4**	**12.2**
Foltête et al., 2012. *Environ.Model.Soft.*	8.0	**15.7**	0.0	6.7	0.0	0.0	1.2
Dyer & Nason, 2004. *Molecular Ecology*	7.4	0.3	0.8	**70.0**	0.0	2.9	3.7
Csardi & Nepusz, 2006. *InterJournal*	7.1	5.4	1.6	**10.0**	6.1	**8.8**	**19.5**
Garroway et al., 2008. *Evolutionary Applications*	4.1	1.0	0.8	**35.0**	3.0	2.9	0.0
Carrara et al., 2012. *PNAS*	3.8	0.0	1.6	0.0	**21.2**	**38.2**	**4.9**
Fahrig, 2013. *Journal of Biogeography*	3.4	**3.5**	**3.9**	3.3	**6.1**	0.0	**3.7**
Campbell Grant et al., 2007. *Ecology Letters*	3.2	0.6	2.3	0.0	0.0	**44.1**	1.2
Hubbell, 2001. *The Unif.Neutr.Theo.Biodiv.Biogeo.*	3.2	0.0	1.6	0.0	**33.3**	**11.8**	**4.9**
Fortuna et al., 2009. *PNAS*	3.1	0.3	0.0	**20.0**	**6.1**	2.9	2.4
Economo & Keitt, 2010. *Oikos*	2.8	1.0	0.8	0.0	**21.2**	**5.9**	**6.1**
Altermatt, 2013. *Aquatic Ecology*	2.7	0.0	1.6	0.0	**6.1**	**35.3**	2.4
Economo & Keitt, 2008. *Ecology Letters*	2.7	0.6	1.6	0.0	**21.2**	**2.9**	2.4
MacArthur & Wilson, 1967. *The Theo.Island.Biogeo.*	2.7	2.2	0.8	0.0	**12.1**	**2.9**	**6.1**
Guimerà & Nunes Amaral, 2005. *Nature*	2.2	0.3	0.0	**3.3**	0.0	0.0	**12.2**
Manel et al., 2003. *Trends in Ecology & Evolution*	2.1	0.6	0.0	**18.3**	0.0	0.0	1.2
Mouquet & Loreau, 2003. *The American Naturalist*	2.1	0.0	0.0	0.0	**27.3**	**5.9**	**3.7**
Brown & Swan, 2010. *Journal of Animal Ecology*	1.9	0.0	0.0	0.0	**6.1**	**32.4**	0.0
Chesson, 2000. *Annual Reviews EES*	1.5	0.0	0.0	0.0	**18.2**	0.0	**3.7**
Dunning et al., 1992. *Oikos*	1.5	**1.6**	**2.3**	0.0	0.0	**2.9**	1.2

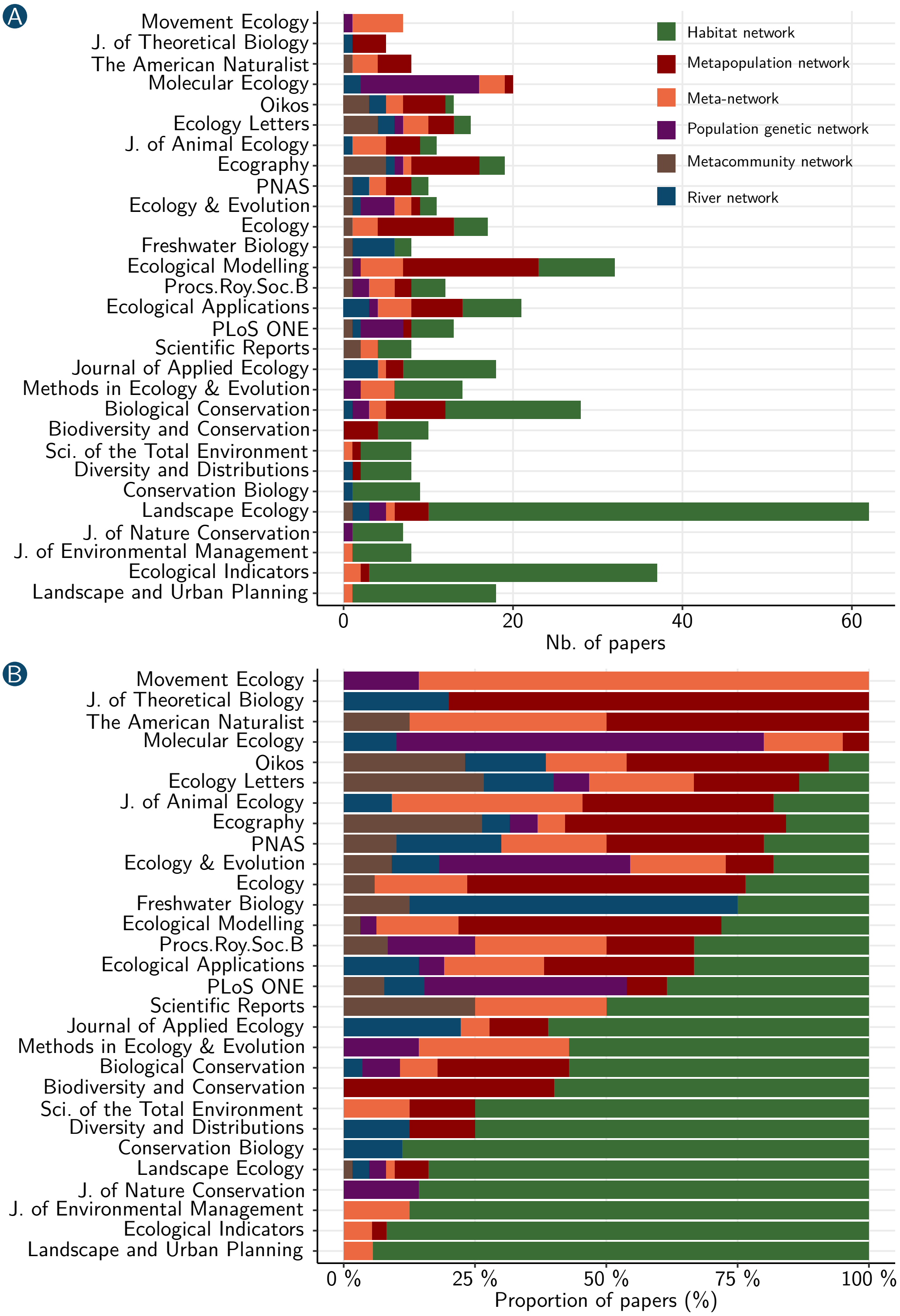

Figure 3: Number (A) and proportion (B) of papers using each type of spatial network published in the journals having published more than 6 papers considered for this review. On panel B, sources are ordered in increasing order of their proportion of papers about habitat networks.

5 Objectives of research using spatial networks and innovative approaches

A few approaches were rather common and reflected the above-mentioned differences in scope and background among research branches. Nonetheless, the most original implementations of each spatial network revealed a wide diversity of uses. Extensions of some approaches to meta-networks have mainly provided solutions to address the specific evolutions of the agenda of each research branch. They have also built bridges favoring their integration into novel frameworks (Figure 4).

Most applied studies using habitat networks evaluate the connectivity of habitat patches connected by dispersal paths in terrestrial or urban landscapes, before finding optimal locations for conservation or restoration. Habitat networks have also been used to assess the connectivity of freshwater habitats (e.g., ponds and wetlands) for one or several species at the same time [25], and of marine habitats [49, 139]. Despite a dominant focus on dispersal, these networks proved useful to model periodic migrations [92, 144]. In a habitat network, the links commonly model movement paths on resistance surfaces using either least-cost path algorithms [3] or circuit theory [91]. This construction step has itself generated an abundant literature and contributed to the integration of empirical data in the construction of habitat networks [48]. Land-cover based resistance surfaces have been increasingly parametrised with genetic data [58] or telemetry data [14], sometimes in combinations with complex movement simulations (e.g., reaction–advection–diffusion modelling [105]). Recent innovations include the use of Markov chains to model individual movements among habitats [16], and Lagrangian particle models [139] or acoustic receivers data [54] for parametrizing marine connectivity. Empirical data have also been used for post-hoc validations of resistance parameters [30, 103, 104], given the urgent need to validate connectivity models [26]. Conversely, habitat network metrics have improved the predictions of species distribution models [98].

Protected area networks being central to conservation strategies, habitat networks whose nodes are protected areas have been ideal tools to assess their coherence, in terrestrial [133] and marine [55] ecosystems. Several studies using metapopulation networks shared this objective, focusing for instance on the viability of populations within the protected area network [76]. Habitat networks have also provided solutions to the mitigation of pipeline impacts [146], the optimisation of carbon sink location for connectivity [109], or the consideration of uncertainty in conservation practice [2]. The connection between habitat network modelling and conservation practice was also visible when habitat networks were included in meta-networks. van Strien & Grêt-Regamey [137] simulated the coupling of human settlement networks with species habitat networks and identified compromises between work-related commuting and biodiversity conservation in developed landscapes [75]. Meta-networks with a habitat network component have made the connection between habitat connectivity and several human-centred objectives, e.g., the walkability of networks in cities [141], wildfire control strategies [7], or the profitability of forestry [10]. The complexity or computational intensity of these works have recently been alleviated by optimisation algorithms (e.g., deep-reinforcement learning [40]), or faster implementations of existing algorithms (e.g., the ConScape Julia library [136]).

To go beyond static approaches, dynamic models have explicitly included changes in the landscape features defining the network, or in the distribution of the populations considered. These approaches proved useful to model the natural or human-assisted spread of invasive populations, pest, or disease [41, 83, 123, 127], as well as range shifts and habitat changes induced by climate change [59, 78]. This emphasis on the dynamics of the network has led to meta-networks making temporal distinctions among multiple layers, to consider species' potential interactions or trajectories over time [50, 88, 133].

Population genetic networks have contributed to the inference of landscape effects on dispersal paths and gene flow (e.g., [35, 58, 121]; see [33, 72] for syntheses), sometimes providing empirical bases to habitat networks [120]. They have been used to represent explicitly the multi-generational nature of gene flow [17] and to compare gene flow patterns across multiple species [52, 114]. Their inclusion in meta-networks has made connections between gene flow patterns and, for instance, the social interaction networks affecting mating regimes [148] or cultural developments in social primates [61]. When nodes are associated with individuals in continuously distributed species, such networks then facilitate the inference of subgroups corresponding to populations [53] or "familial networks" [90].

In the research branches using metapopulation, metacommunity, and river networks, the construction of the network was less central than understanding the consequences of its structure for the studied biological responses. Interestingly, 21 %, 15 %, and 6 % of the studies using river, metacommunity, or metapopulation networks, respectively, adopted an experimental approach based on microcosms [8, 69, 111], mesocosms [129], or lab experiments [77] with, for instance, protists as a model [60] (Table S2). The frequency of experimental works could explain the stronger use of theory in these research branches, as a way to align the tested predictions with the experimental design. Experiments and a frequent use of simulations made it possible to test the role of network topology on, for instance, the synchrony and stability of metapopulations [145], their extinction time [39] and spread speed [111], or the predator-prey dynamics [60] and invasion dynamics [69] of dendritic river networks. Similarly, considering the topology of metacommunity networks has been key to uncover how spatial constraints on dispersal affect the diversity, stability, and coexistence of species [24, 128, 122, 131, 147]. Recent original approaches include the work by Fahimipour et al. [45], which used game theory and mathematical network models to uncover coexistence mechanisms, the experimental approach by Kuhn et al. [77] on bacterial experimental metacommunities, or the study by Barta et al. [11] using a small-scale network of small ponds of same age to compare the diversity of actively *versus* passively dispersing organisms.

Meta-networks based on metacommunity networks have mostly consisted in including species interaction networks within communities. These interactions can be antagonistic (e.g., trophic [102], parasitic [6]) or mutualistic (e.g., seed dispersal [82, 96, 132]) (Figure 4). Although meta-networks have often built on previous approaches mobilizing spatial networks, some applications were unique and difficult to classify. This was partly due to the adoption of spatial networks by other fields of ecology initially focused on aspatial networks. For instance, the papers by Ryser et al. [115] and Mougi [93] show how the consideration of space changes previous predictions about the species-area relationship for food webs, or paradoxically makes the dynamics of these networks more predictable. Some meta-networks also distinguish their nodes and links according to their habitat type [119] or movement type [106]. Similarly, the meta-ecosystem framework introduced by Harvey et al. [67] provides a comprehensive model of the processes and flows connecting multiple ecosystems at large scales. In meta-networks, not all components need to be spatially-explicit. For instance, the species-habitat models proposed by Marini et al. [87] relate each species to the habitats it occupies, allowing for habitat-level and species-level analyses of landscape change impacts (see [79]). In some approaches, each patch is related to all the individuals visiting it [101], or to the eco-evolutionary mechanisms or mating system affecting individuals within it [18, 51]. Finally, movement ecologists have developed meta-networks using data on the spatial co-occurrence of individuals and their different movement behaviours [22, 73, 86].

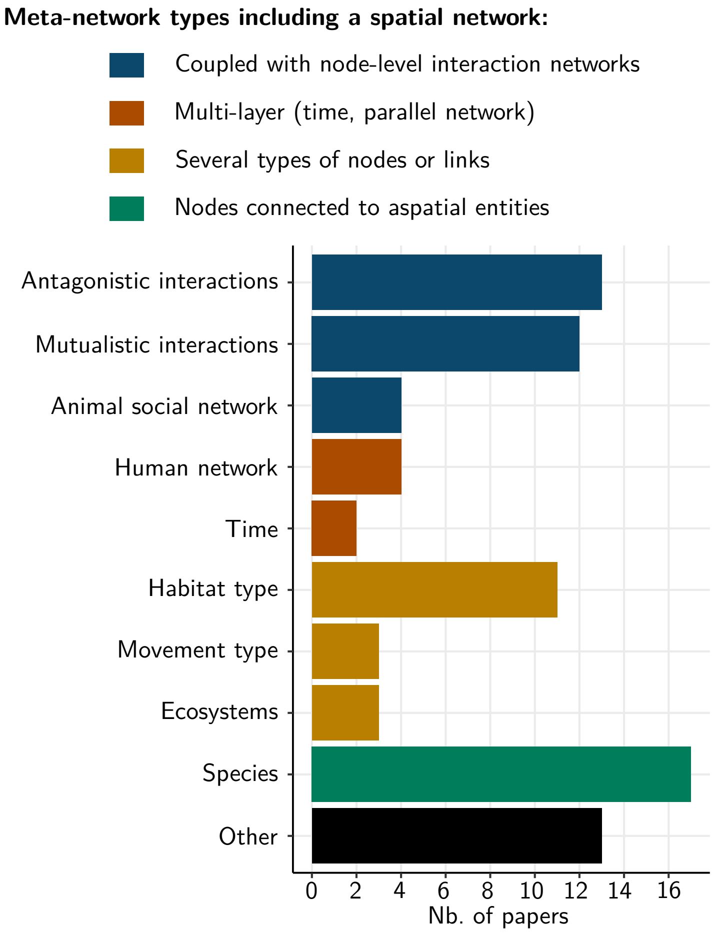

Figure 4: Number of papers about meta-networks of each type. Meta-networks include a spatial network which is either related to node-level interaction networks (blue bars), or other spatial layers (orange), has several types of nodes or links (yellow), or whose nodes are connected to aspatial entities (green). Interactions include antagonistic interactions (trophic, parasitic), mutualistic interactions (pollination, seed-dispersal), and animal social networks. Multi-layer networks include temporal layers or human infrastructure networks. Node types can represent habitat types or ecosystems, and link types distinguish movement types. Aspatial entities related to nodes are species. The "Other" category includes review papers and meta-networks not falling in previous categories.

6 Conclusions

I reviewed the ecological literature published about spatial networks in the last 25 years to assess the level of integration of its main research branches. The gathered corpus revealed that distinct spatial networks are associated with research works diverging in their approaches and objectives. While some research branches tended to emphasize the methods used for assembling and analysing the network, others focused on the influence of the network for the dynamics of biological entities. This source of differentiation partly matched an even stronger opposition distinguishing studies having conservation purposes from those investigating theoretical questions. Habitat networks, the most frequently used in the corpus, were usually dedicated to connectivity assessments and predominant in journals with applied scopes. The abundant literature on their construction and analysis methods has significantly improved connectivity modelling. A more frequent use of empirical data now helps to parametrise and validate these models. In contrast, studies using networks of metapopulations, metacommunities, or river branches have followed the evolution of questions asked in ecology about community assembly and population dynamics. They revealed the ecological role of some spatial patterns uniquely described using network theory (e.g., dendritic structures, modularity, centrality). These studies were more frequently experimental and relatively similar despite the diversity of study systems, confirming that ecology is increasingly concept-oriented rather than taxon-oriented [113].

Overall, these results align with the divergence of ecology and conservation biology observed by

Hintzen et al. [68]. Whereas theoretical studies need to recall their applied implications, the reverse is not necessarily true, which can amplify the disconnect. This can also result from the perception that fundamental findings will not make a difference for conservation practice in the short term. Furthermore, when journals specialize on some topics and authors develop in turn publishing preferences, they can become echo chambers rather than scientific agoras [126]. Eventually, this can lead to research silos, with potential risks for the research on spatial networks. For instance, when these tools are used for conservation purposes, they often help identify the most connected or isolated habitat patches. This guides their conservation or restoration with the implicit objective of favoring population survival and biodiversity. Yet, recent theoretical advances can help identify contexts in which this practice would not be the most successful because other processes than dispersal have stronger influences on ecological responses, or because connectivity has a crucial yet not empirically detectable influence (see Box 2 and Figure 5 for a demonstration based on population genetic and metacommunity simulations). As such, the mechanisms behind pattern-process relationships should be given further consideration to bridge the methodological developments of spatial networks with recent theoretical knowledge. Restoration ecology has recently made such a shift to help design experiments on the success of restoration strategies because considering community assembly mechanisms can be crucial in this context [138]. Initially, the framework introduced by Urban & Keitt [134] was closely linked to the early stage of metapopulation theory. Consequently, even if conservation practice has its own practical constraints and modelling challenges, applied studies on spatial networks should stay similarly connected with theoretical advances.

On a more positive note, the diversity of spatial network applications (including the genericalled called "spatial networks" or "dispersal networks") is a clear sign that they prove useful to many ecologists, even outside the research silos suggested above. Besides, the bridges generated by meta-networks and other integrations of existing approaches have helped to focus not only on dispersal, but also on what happens in the nodes of spatial networks (e.g., species interactions, mating systems, habitat patch heterogeneity). Fortunately, the disconnection of the research branches using spatial networks is relative. By being aware of the full range of existing approaches, one can more easily find the methods and theoretical frameworks they need for answering their questions. Furthermore, the gaps identified in one branch might have already been addressed in another, or could be bridged by connecting existing approaches (e.g., in the form of a meta-network). Moreover, this review might have missed relevant references given that the most original ones are also the most difficult to retrieve with common keywords. Assigning a type of spatial network to each study may have slightly amplified the silo effect and was not always straightforward. Several studies could have fallen into several research branches and meta-networks were difficult to describe, which confirms that despite marked research branches, the use of spatial networks is still diversified in ecology. Interestingly, the term "network" was frequent in studies doing analyses that could have been done without invoking network theory. This should encourage every user to question the unique added value of network theory for their work and use spatial networks in the most adapted contexts.

Finally, future applications could take inspiration from what is done with networks outside spatial ecology. Recent network-based models have helped to infer node clusters (e.g., stochastic block model [89]), networks links [124], or to model social animal networks and disease spread [4, 125]. Spatial applications of the graphical lasso [31], self-organised maps [71], and the large toolbox developed for multi-layer networks [15] could also find applications in ecology. As stressed above, these methodological developments should respond to research objectives and keep track with theoretical advances, not the reverse. Accordingly, recent works on the metapopulation framework [95], guidelines on how to integrate multiple species in connectivity models [142], or the new connections made between population genetics and community ecology [99] should be scrutinized. Paradoxically, it seems that cutting-edge research on spatial networks should first use existing approaches from within and outside spatial ecology and, more importantly, connect them.

Box 2: Interpreting biological responses to dispersal in spatial networks

Ecologists commonly follow the long tradition of hypothetico-deductivism in biology. As such, they formulate hypotheses and test the predictions they entail in their study systems using a wide range of observational and, more rarely, experimental approaches. Given the frequent focus on dispersal of research on spatial networks, it often tests hypotheses about the effect of connectivity (in this context, how dispersal is constrained by the network) on biological responses ranging from genetic or species diversity to extinction time or synchrony. Completely isolated populations are subject to extinction and genetic drift. Therefore, it is usually predicted that population genetic diversity and community species richness will increase with the connectivity of the patches they occupy. Observing empirically such a trend would tend to give more credence in this hypothesis, and be translated in the following way: connectivity matters and we need to conserve it to preserve biodiversity. This reasoning can have limitations, especially when it comes to interpreting the absence of such a trend. This is when the theoretical framework in which the study is embedded matters most. For instance, it is known from population genetic studies that both the absence and excess of gene flow will flatten the relationship between the relative connectivity of a population and its genetic diversity, due to complete isolation and divergence through drift in the first case, and quasi-panmictic populations with homogeneous allele pools in the second. Only for intermediate dispersal rates and dispersal distances will the predicted correlation emerge, as simulated on Figure 5. After population genetic simulations for three dispersal rates, population allelic richness was correlated to the "Flux" network-based connectivity metric (see Supplementary information for the details). In all three cases, connectivity matters but its effect is empirically detectable in the form of a correlation only when dispersal is a limiting factor of diversity in the most isolated patches.

Similarly, under neutral formulations of community assembly, species diversity patterns are the results of speciation, local ecological drift (extinction), and dispersal among communities; environmental filtering and competition affecting all individuals regardless of their species identity. When dispersal and extinction are the main community assembly processes, a positive correlation is expected between species richness and the connectivity of a community. Yet, as in the genetic case, this correlation is only strong for intermediate dispersal rates, as simulated on Figure 5 using the metacommunity simulation framework of Khattar et al. [74]. However, including species sorting and a stabilizing form of competition among species affects the trend as well as the overall richness of communities. Thus, interpreting the trend and levels of diversity in the light of dispersal alone could lead to incorrect identifications of the main processes affecting diversity. For instance, very different levels of diversity can be expected for strikingly different dispersal rates when other processes are at play. In sum, failing to acknowledge the comprehensive approach of community assembly brought by metacommunity theory could compromise the conclusions of works using networks if they are only focused on dispersal when formulating predictions and interpreting the results. This could affect the conservation-oriented translation of these results because even though dispersal always leaves an imprint on biodiversity patterns, this is not always the dominant process, nor the one to manipulate for reaching conservation goals.

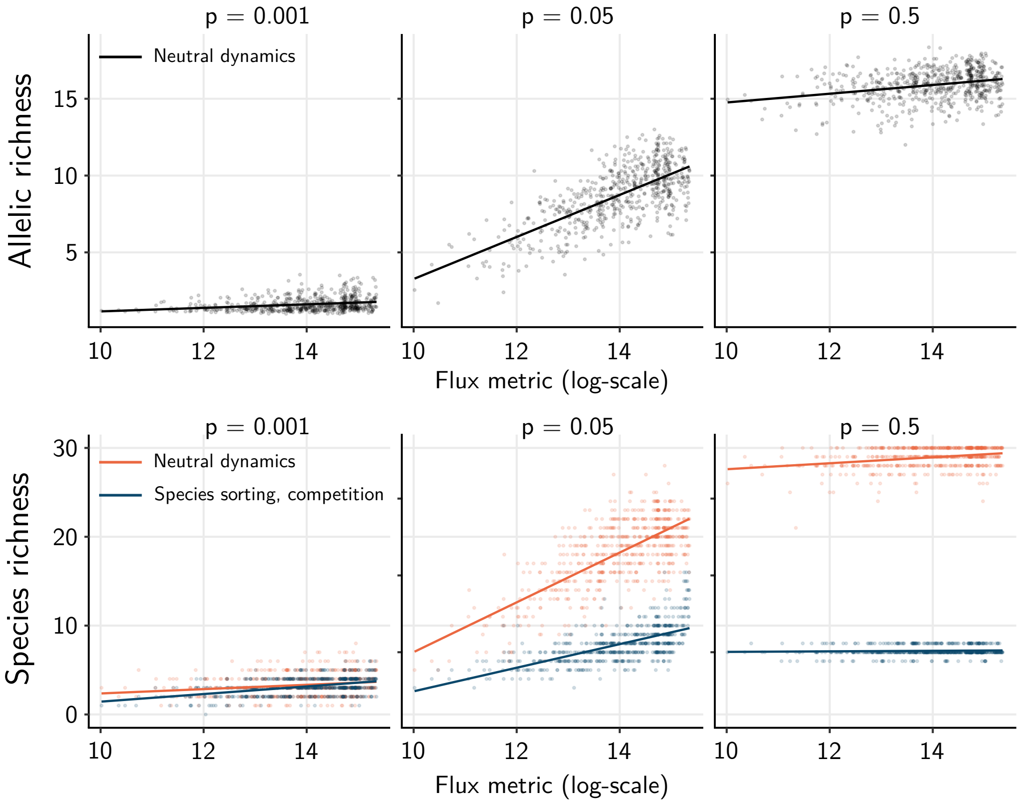

Figure 5: Relationships between the Flux metric computed at the node-level for each forest patch displayed on Figure 1 (in log-scale) and either the allelic richness of populations (top panels) or species richness of communities (bottom panels) simulated in these patches under the action of different ecological or evolutionary processes. Vertical panels distinguish simulations performed with varying dispersal rates and probabilities ($p = 0.001$, 0.05 or 0.5). Neutral population genetic simulations (black trends) included the effect of genetic drift and dispersal-driven gene flow. Neutral metacommunity simulations (orange trends) included the effect of dispersal, stochastic extinction (i.e., ecological drift), and equal intra- and inter-specific competition. The non-neutral metacommunity simulations (blue trends) included species with different niches subject to species sorting, stronger intra- than inter-specific competition (stabilizing), as well as dispersal and stochastic extinction. Each trend summarizes the linear relationship between the Flux metric and the diversity response for $n = 610$ patches. See simulation details in the Supplementary Information.

7 Key references

- Arancibia, P. A. & Morin, P. J. (2022). Network topology and patch connectivity affect dynamics in experimental and model metapopulations. *Journal of Animal Ecology*, 91(2), 496–505
  Combination of simulations and experimental protist metapopulations showing how the interplay between colonization/extinction rates and network topology mediates rescue effect and metapopulation dynamics

- Cerecedo-Iglesias et al. (2023). Resource predictability modulates spatial-use networks in an endangered scavenger species. *Movement Ecology*, 11(1), 22
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  Presentation of the "ecological network dynamics framework", modelling coupled spatial and interaction networks in dynamic landscapes

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  Presentation of the meta-ecosystem model and its possible applications.

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  Introduction to species-habitat networks, where several species are connected to the habitat patches they use at landscape-scale.
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  Study showing the rewiring of Caribou movement networks following forest logging, implementing original simulations of movement and landscape changes, validated with telemetry data
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  Studies showing how the heterogeneity of dispersal networks across species can favour unexpected coexistence patterns in a competitive context

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Ethics statements

Conflict of Interest

I declare no conflict of interest.

Human and Animal Rights and Informed Consent

This article does not contain any studies with human or animal subjects performed by the author.

Data availability statement

The data and codes used for the literature review are available at:
https://gitlab.com/psavary3/SpatialHabNetworksReview.

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