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Using ecological networks to answer questions in global biogeography and ecology

Abstract

Ecological networks have classically been studied at site and landscape scales, yet recent efforts have been made to collate these data into global repositories. This offers an opportunity to integrate and upscale knowledge about ecological interactions from local to global scales to gain enhanced insights from the mechanistic information provided by these data. By drawing on existing research investigating patterns in ecological interactions at continental to global scales, we show how data on ecological networks, collected at appropriate scales, can be used to generate an improved understanding of many aspects of ecology and biogeography—for example, species distribution modelling, restoration ecology and conservation. We argue that by understanding the patterns in the structure and function of ecological networks across scales, it is possible to enhance our understanding of the natural world.

1 | INTRODUCTION

At the global scale, biogeography and ecology have primarily focused on understanding the distribution and abundance of species. This work has improved our fundamental understanding of species distributions (local to global: Matthews et al., 2017) and highlighted the large number of abiotic and biotic processes that influence ecological processes (Morris et al., 2020). What is generally missing from global assessments, however, is data on ecological interactions (e.g. competition, predation, mutualism and parasitism). Investigating the patterns of local ecological interaction networks across broad biogeographical scales is challenging due to the substantial investment in time and resources associated with sampling ecological networks (e.g. timed observations of insects visiting flowers and gut

content or faecal analysis; Jordano, 2016). Yet, understanding ecological interactions at large spatial scales is crucial for determining the structure, resilience and functioning of ecosystems (Kissling & Schleuning, 2015).

Ecological networks are the 'tangled bank' of interactions between organisms, populations, communities and ecosystems (Guimarães, 2020). The fundamental units of these networks are interspecific interactions (on which we primarily focus here), which arise from ecological and evolutionary processes across different spatial and temporal scales (Segar et al., 2020). Theoretically, we understand how and why ecological interactions vary in space and time (Poisot et al., 2012; Poisot et al., 2015), yet empirically we are just scratching the surface when it comes to exploring and understanding biogeographical variation in ecological networks (Gravel et al., 2019).

Here we propose that data on ecological interactions at large spatial scales offer the potential to gain an improved understanding of ecological systems. First, we highlight recent methodological advances and how they can be used to generate highly replicated, spatially expansive datasets. We then go on to explore existing research and identify advances that could be generated by combining ecological network data with current macroscale research priorities in ecology and biogeography.

2 | GLOBAL ECOLOGICAL NETWORK DATA

Data on ecological interactions are collected at high resolution over small spatial scales and have typically focused on a single interaction type (Ings & Hawes, 2018). Very few studies have collected replicated data at continental to global scales. Yet, we argue ecological interaction data at these scales are necessary to address pressing environmental challenges.

There are two options for generating datasets of ecological interactions at biogeographical and global scales: (i) collating and manipulating existing site and landscape scale data; or (ii) collecting new highly replicated data at appropriate spatial resolution and coverage.

With regards to the first option, substantial work by the research community has collated ecological network data into
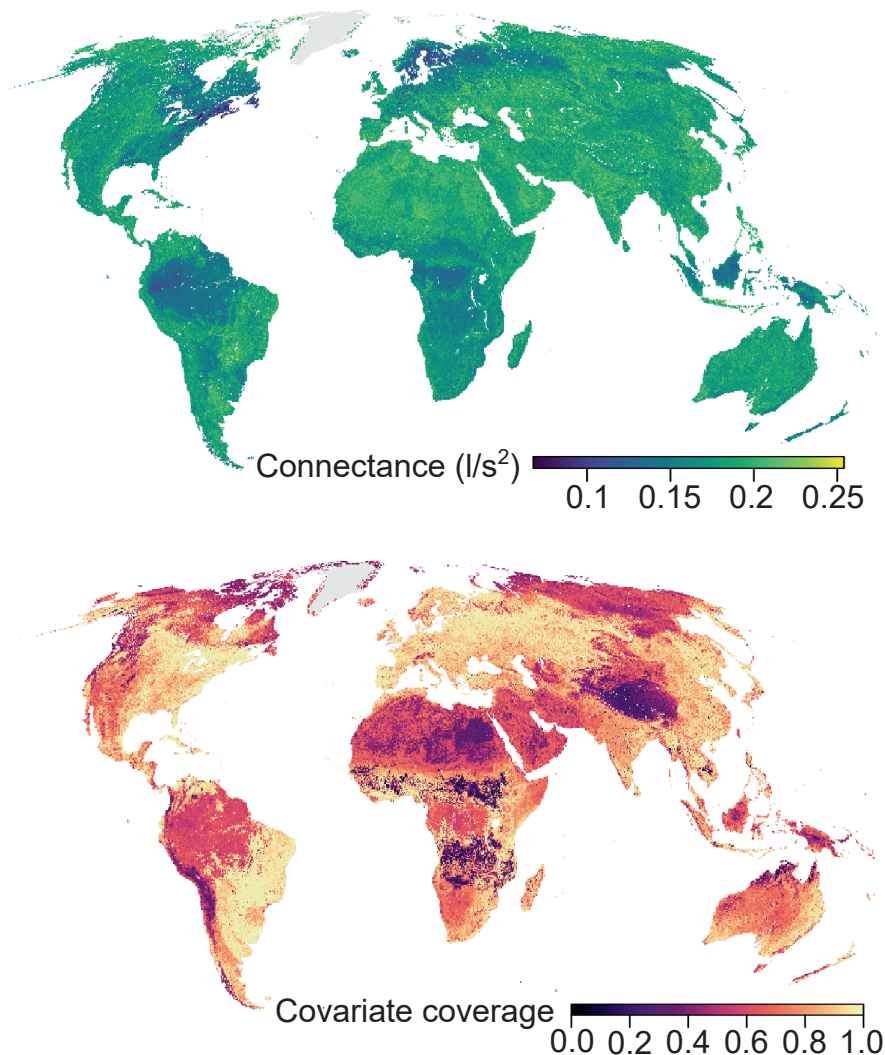

FIGURE 1 Global data layers for (a) connectance of plant–herbivore networks and (b) relative coverage of environmental covariate data (a measure or proxy for uncertainty in predications). The values of 0 in (b) represents no coverage and 1 indicates complete coverage (i.e. complete coverage of environmental covariates and network data). Maps are displayed using the Mollweide projection (ESRI: 54009)

repositories, including Mangal (Vissault et al., 2019), Web of Life (Web of Life, 2020), Interaction web database (IWDB, 2020) and GloBI (Poelen et al., 2014). Although the spatial coverage of these data is not exhaustive and data are restricted to certain habitats in well-studied ecosystems (Poisot et al., 2021), methodological developments mean it is possible to fill these gaps. In Box 1, we show how a predictive framework using widely available global data layers of environmental variables (e.g. temperature, soil characteristics and net primary productivity) can extrapolate data from observation sites to those with similar environmental and biological conditions. A more mechanistic approach has also been recently proposed, providing an option for the prediction of ecological networks based on limited data (Strydom et al., 2021).

The second option is to collect data on ecological interactions at an appropriate scale (e.g. habitat, ecosystem or landscape) but with carefully designed replication within and between biogeographical regions. This is possible through the formation of international collaborations between researchers across the globe using standardised methods to sample ecological networks. Such research is more feasible than ever with the advent of new methods.

Molecular techniques, in particular, provide an opportunity to collect the highly replicated and spatially expansive datasets (Bohan et al., 2017; Ma et al., 2018). There are also other approaches which make use of existing resources from which ecological interactions can be sampled, such as image repositories (i.e. Google images or iNaturalist; Doherty et al., 2021) and text scraping from web pages (Jarić et al., 2020).

Below, we investigate the use of global scale data on ecological interactions to (i) identify the mechanistic basis for universal ecological patterns (e.g. understand spatial and temporal variation in biodiversity–ecosystem functioning relationships); (ii) link ecology and evolution using network theory (e.g. predict how invasive species integrate into native ecosystems and ecological networks); (iii) integrate ecological networks into biogeography and enhancing the accuracy of species distribution models; (iv) target biomonitoring as well as provide new metrics to measure biodiversity and ecosystem functioning; (v) forecast ecological responses to environmental change; and (vi) inform conservation and restoration decisions, and provide new methods for planning and management.

BOX 1   Up-scaling ecological network data for use in ecology and evolution

A limit of current large-scale research on ecological networks is the patchiness and poor resolution of data, as well as an absence of suitable methods to down- and up-scale data to appropriate scales (i.e. 10 km^2 resolution data used in global studies). Here we present a method for generating global data for ecological interaction networks at ~1 km^2 resolution (see Materials S1 for the full methods). We collated data on plant–herbivore networks from Web of Life (www.web-of-life.es) and Mangal (www.mangal.io). For 144 plant–herbivore networks across the globe, we calculated connectance (observed links as a fraction of potential links) and extracted environmental covariate data from 31 global data layers (van den Hoogen et al., 2019). We constructed relationships between connectance and environmental covariates using random forest models. In this example, we did not control for influential factors such as network size (i.e. number of species); however, it is possible to standardise predictions (e.g. using z-scores) to produce more robust maps of ecological network properties. Through iteratively altering the set of covariates and model hyperparameters, we evaluated the strength of models using k-fold cross-validation (k = 10) and selected the best performing model that had the highest predictive ability, while limiting multi-collinearity, overparameterisation and overfitting. Using this model, we predicted the connectance of plant–herbivore networks across the terrestrial surface of the globe (Figure 1a). The model accurately predicted the connectance ($R^2 = 0.89$), and there was a reasonable coverage of environmental covariates (Figure 1b). The relationships between explanatory variables and connectance, as described by correlations from generalised linear mixed models (Figure 2b,c), were significant and ecologically sensible.

There are a number of caveats associated with extrapolating data across unsampled regions based on environmental characteristics. First, we assumed that ecological network data are representative of the wider region (i.e. the ~1 km^2 pixel). This may not be the case for a variety of reasons, and it is likely that the networks represent only a subset of the species and interactions present. Moreover, ecological networks vary on micro to macro scales, and the extent to which data represent a 1 km^2 pixel depends on the scale of the sampling used for network construction. Second, we assume that the environmental factors are causally related to ecological networks, as we then use correlative relationships to extrapolate beyond the regions in which data are present. If relationships are simply correlative, then our estimates across unsampled regions may not be accurate. Finally, the properties of ecological networks are strongly influenced by method of network construction, sampling effort and research focus (i.e. most studies focus on a subset of organisms, such as invertebrate pollinators). Study metadata, however, could be used as covariates in analyses to account for variation generated by different field methods or sampling completeness.

3 | DEVELOPING A MECHANISTIC UNDERSTANDING OF ECOLOGICAL PATTERNS

Understanding ecological interactions at large spatial scales provides the potential to assess universal patterns in ecology—for example, island biogeography theory and species interaction–area relationships (Galiana et al., 2018), but also variation in ecological functions such as pollination (Trøjelsgaard & Olesen, 2013) and seed-dispersal (Dugger et al., 2019). Although patterns in global data on ecological interactions have been investigated, they have not often been used to provide a mechanistic understanding of ecosystems. Below, we highlight several areas of research in which global data on ecological networks could provide critical insights.

3.1 | Biodiversity–ecosystem functioning

Linking biodiversity and ecosystem functioning (BEF) continues to be a challenge in ecology, especially at broad spatial scales (Gonzalez et al., 2020). A variety of behaviours, scale-dependencies and contradictory results have been identified in studies (Pennekamp et al., 2018; Thompson et al., 2018). Ecological networks provide an

opportunity to gain mechanistic knowledge regarding BEF relationships (O'Connor et al., 2017). First, interactions influence the biodiversity or species richness present in the landscape (García-Callejas et al., 2021). Second, and perhaps more fundamentally, interactions between species are responsible for ecosystem functioning across scales (Harvey et al., 2017), and many interactions are in fact ecosystem functions (e.g. pollination, predation and seed dispersal). Despite the known importance of ecological interactions in BEF research, the translation of species interactions into community assembly and structure, as well as ecological processes (i.e. resource complementarity; Thompson et al., 2021), over large spatial scales is an area of research that remains poorly understood. By understanding large-scale variation in BEF, we could gain an improved causative knowledgebase, but also provide tools for decision-making and management (e.g. estimating the levels of diversity required across the globe to achieve a necessary level of certain ecosystem functions and services).

3.2 | Complexity–stability debate

Complexity and stability are heavily debated ecological concepts. Contradictory results from theoretical, experimental and
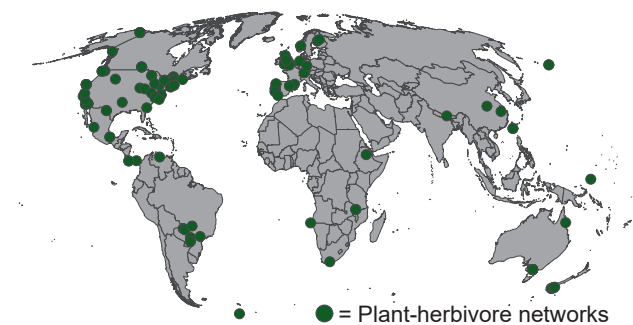
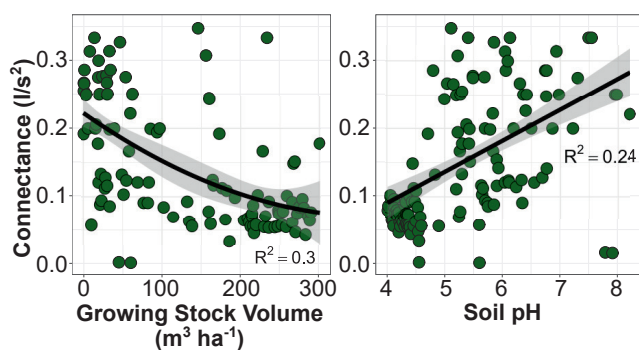| Variable	R²
Growing stock volume	0.30
Aboveground biomass	0.28
Deciduous broadleaf tree cover	0.28
Surface soil pH	0.24
Tree density	0.24

FIGURE 2 Global plant–herbivore network data and relationships between environmental covariates and network connectance. (a) The geographical distribution of plant–herbivore networks ($n = 144$). The map is displayed in the Mollweide projection (ESRI: 54009). (b) Dominant explanatory variables in the best performing predictive model as described by R^2 values for correlations between connectance and variables from the random forest models. (c) Correlations between connectance and two of the environmental covariates from the best performing model

environmental gradients would have the potential to achieve a greater level of causality than many previous field-based studies. This would especially be the case when the multiple types of direct and indirect interactions, and the ecosystem functions for which they are responsible, are assessed over large scales. By investigating complexity–stability relationships across gradients of network complexity (i.e. single to multiple types of interactions), as well as across different scales (i.e. local to regional) it may be possible to enhance our understanding. Furthermore, it would allow for a thorough investigation of the scale dependence of these relationships. Taking this idea a step further, it is possible to use spatial networks (Gonzalez et al., 2017) and merged socio-ecological networks (Rubiños & Anderies, 2020) to understand broader complexity, stability and resilience.

3.3 | Response diversity

Individual species' responses to perturbations both influence, and are influenced by, the structure of ecological networks. Indeed, the diversity of species responses in a community (response diversity; Elmqvist et al., 2003) has been shown to vary in response to both mutualistic and antagonistic interactions (Dell et al., 2019). This can be intuitively explained by the fact that the structure of the ecological network in which an organism interacts determines potential responses, and vice versa (Mori et al., 2013).

Response diversity may be strongly influenced by ecological interactions at large spatial scales: (i) interacting species are more likely to respond in a similar way than those which do not directly interact (e.g. species linked mutualistically may respond similarly; Bartomeus et al., 2011); (ii) species in the same network modules are likely to respond in a similar way (e.g. spatial modules such as habitats, or interspecific modules such as groups of organisms interacting to a greater extent with one another; Guimarães, 2020); and (iii) cascading effects through ecological networks (i.e. rippling indirect effects resulting from species extinctions) may lead to similar responses of functionally distinct species within a community (e.g. bottom-up trophic cascades, where the loss of a primary resource may also generate losses of both generalist and specialist consumers through intermediate species; Gawecka & Bascompte, 2021). Investigating these interactive responses at large spatial scales is an important frontier in understanding how ecosystems respond to change (Bartley et al., 2019).

3.4 | Scaling in network ecology

An outstanding question and research priority is the effect of scale of ecological networks. Recent work has shown that like many other ecological phenomena there is a strong element of scale dependence in ecological networks (Galiana et al., 2022). For example, in host-parasitoid networks, climatic variables were associated with changes in connectance, consumer diet overlap, diet breadth and resource

observational studies have long arisen, especially around the linkages between complexity and stability—the complexity/diversity–stability debate (Allesina & Tang, 2015). Ecological interactions play an important role and are often the root of the debate (i.e. whether a greater level of connectance and/or complexity within species interaction networks promotes higher or lower stability; Landi et al., 2018). Using data and theory from network ecology at a range of scales, new findings have been provided in this debate, and it is clear that different interactions (predator–prey, mutualistic and competitive) are either stabilising or destabilising (Allesina & Tang, 2012; Barnes et al., 2018; Emary & Evans, 2021).

Integrating global scale data into this ongoing debate would enable an improved understanding of universal patterns. Furthermore, assessments of ecological networks and their complexity–stability relationships across space, between continents or along large

vulnerability at local scales, yet at a larger regional scale these variables were not related to network properties (Galiana et al., 2019). Using network theory, we can directly confront the issue of scale and track its effects from local processes to global patterns. As an example, species extinctions at the site level rewire food webs generating different individual-level responses. Equally, changes in the species distribution of individuals alter network structure and how networks across sites respond to change (Alexander et al., 2016).

We suggest using high-resolution assessments over large spatial scales to improve our understanding of ecosystem structure and function. By comparing the properties of ecological networks at different spatial resolutions (50, 10 and 1 km^2), it is possible enhance fundamental knowledge (Galiana et al., 2021), but also determine the necessary scales for robust decision-making based on ecological network data.

3.5 | Ecological resilience

Networks can be used to investigate ecological resilience across systems and scales (populations, communities, landscapes, regions, continents and globally). Existing work has focused on assessing spatial variation in ecological resilience at the local scale (i.e. the resilience of distinct interaction networks), with examples for mutualistic networks showing that human disturbance and climate warming have different impacts on pollination and seed dispersal network resilience (Nagaishi & Takemoto, 2018). Similar results across other types of interaction networks, however, cannot be assumed. As such, it is now imperative that we increase our understanding of how wider interaction types may be resilient (e.g. predator–prey, competition, facilitation, among others), but also how networks of multiple interaction types (i.e. multilayer ecological networks), such as those actually occurring in natural systems, respond. At large scales, network theory could be applied to spatial networks (e.g. interactions of species, habitats or nations in geographical space) to understand how the movement of individuals may connect different ecological systems and enhance resilience across scales (Allen et al., 2016). Developing this understanding for ecological systems at a global scale will be difficult owing to their significant complexity; however, it is crucial in efforts to mitigate the effects of global environmental change.

4 | LINKING ECOLOGY AND EVOLUTION THROUGH NETWORKS

Ecological networks are a product of the interactions of ecological and evolutionary processes (Segar et al., 2020). Yet, ecology and evolution are not often incorporated together in ecological networks at large scales (but see Melián et al., 2018). The increasing coverage of both ecological and evolutionary data (e.g. birds; Jetz et al., 2012), however, means that there is a significant potential for eco-evolutionary research at continental and global scales. Combining ecology and evolution at global scales,

BOX 2 Effects of ecological interactions on the distribution and abundance of species

Our current understanding of how ecological interactions affect the distribution of species highlights a number of effects: (i) abrupt range limits due to allopatry (Case et al., 2005); (ii) manipulation of the environment or abiotic conditions by one species facilitates colonisation or co-occurrence by another (i.e. successional processes); (iii) patchy distributions in relation to strong species interactions (e.g. territoriality and competitive exclusion) (Gotelli et al., 2010); and (iv) antagonistic interactions alter the relative abundance of species through direct (e.g. predation, parasitism, facilitation and mutualism) and indirect effects (apparent competition). Current approaches incorporating ecological interactions primarily use co-occurrence to determine the influence of biological processes on the distribution and abundance of a species. There are, however, a range of issues with such approaches (Blanchet et al., 2020), and it is unclear how useful these methods can be as they lack substantial mechanistic bases.

Using an example, we highlight how species interactions could be included directly when investigating species distributions into the future. It should be noted that this approach assumes that we have suitable spatial information on network structure at an appropriate scale. In the example, Figure 3, we present a theoretical bipartite network of plants and pollinators (Figure 3a). In this network, there are mutualistic interactions between plants and pollinators, but also antagonistic interactions in the form of interspecific competition between pollinator species. In this simplistic example, mutualistic interactions promote the co-occurrence of plants and pollinators, and antagonistic interactions cause competitive exclusion in pollinator assemblages.

Here we use BAM diagrams (Soberón & Peterson, 2005; Figure 3b,c) to visualise the effects of these direct species interactions on the distribution of a pollinator across a hypothetical landscape matrix. A (geographical area with abiotic conditions suitable for the species) and M (geographical area accessible to the organism) are the same in both cases (Figure 3b,c), yet B differs. In the first example, B_m is the geographical area with an interacting plant species present. For the second example, B_m is the same, yet B_a is the additional negative influence of competitors—here this represents the geographical area which a pollinator cannot inhabit due to interspecific competition and competitive exclusion. It is clear in both examples how layering different types of species interactions may aid in more accurately predicting the distribution of species across a range of spatial scales.
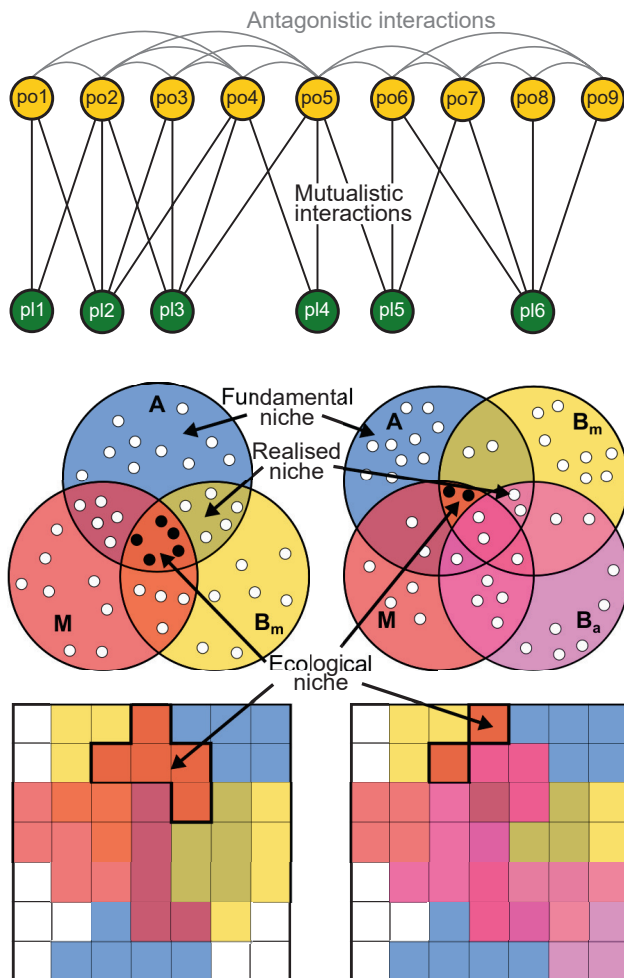
FIGURE 3 How ecological networks can affect species distributions. (a) A theoretical network of plants (pl) and pollinators (po) with a series of mutualistic and antagonistic interactions. (b, c) BAM diagrams and landscape matrices for the distribution of po9 including (b) only mutualistic species interactions (B_m) and (c) both mutualistic (B_m) and antagonistic (B_a) species interactions. In both (b) and (c), A is the geographical area with abiotic conditions suitable for the species and M is the geographical area accessible to the organism. Note that the distribution of po9 is more constrained when we include the effect of antagonist interactions in our approach

using approaches such as adaptive and dynamic network models (capturing feedbacks in trait evolution, species abundances and interactions; Raimundo et al., 2018), provides an opportunity to advance our understanding macroecological processes and patterns. For example, using phylogenetically structured networks (Evans et al., 2016), it may be possible to predict the role an invasive species will play in an ecosystem into which it is introduced (Emer et al., 2016). Further to this, eco-evolutionary analyses at large spatial scales offer the potential to understand multiple drivers of ecosystem processes. For example, biogeographical variation in phylogenetically structured hummingbird–plant networks showed that specialisation and modularity in networks

was influenced by intraspecific competition in closely related hummingbird species—suggesting a stronger co-evolutionary association than determined from site and landscape scale studies (Martín González et al., 2015).

5 | INTEGRATING ECOLOGICAL NETWORKS INTO THE FIELD OF BIOGEOGRAPHY

Ecological interactions are less commonly studied in biogeography due to the challenges associated with data collection (Kissling et al., 2012). Existing large-scale research, however, has shown how the structure of ecological networks, as well as the identity and strength of intraspecific and interspecific interactions, directly influences species distributions and abundances (Box 2) and displays unique biogeographical signatures.

5.1 | Building ecological interactions into species distribution models

Early studies that included ecological interactions demonstrated significant improvements in the accuracy of species distribution models (e.g. Araújo & Luoto, 2007). From a fundamental biogeographical perspective, it is therefore critical to understand ecological interactions at large scales when investigating the distribution and abundance of individual species. As such, studies have developed methods such as joint species distribution models to account for the effects of co-occurring species (Dormann et al., 2018). These methods, however, assume that co-occurrence is an indicative of an interaction between species, which we know is not always the case (Blanchet et al., 2020). Several studies have attempted to integrate data on ecological interactions into distribution models, using different methods. Some have refined the predictions from models using biotic interactions (Staniczenko et al., 2017), while others have implicitly included antagonistic interactions by preventing the co-occurrence of different taxa (Gavish et al., 2017). Future studies should continue to focus on directly integrating ecological interactions, and their strengths (e.g. visitation frequency in plant–pollinator networks). Yet, one key remaining challenge is characterising and incorporating the full assortment of ecological interactions that influence species distributions.

5.2 | Ecological interactions as biogeographical variables

Various measures of ecological interactions could be used in biogeography: (i) interaction identities (i.e. specific interactions between species); (ii) spatial rewiring and turnover of interactions (i.e. interaction beta-diversity); and (iii) network properties (i.e. topological metrics such as connectance or robustness). Indeed, recent studies have

TABLE 1 Research priorities, methods, specific examples of integrating large-scale data on ecological interactions across biogeography and ecology

Area of research	Research priorities	Example(s)
Biodiversity–ecosystem functioning	What are the patterns and spatiotemporal variation in BEF relationships?	Investigating the influence of multiple interaction types across biomes
Complexity–stability debate	Why are there contradictions in existing research?	Studying real-world systems with different levels of complexity (i.e. gradients of complexity across ecosystems or biomes)
	Are there differences in complexity–stability relationships between biomes?	Assessing variation in complexity–stability relationships in ecological networks along environmental gradients and between biomes
	How do complexity–stability relationships scale?	Relating complexity and stability across spatial ecological networks covering different spatial scales (e.g. regional, continental and global)
	Are there complexity–stability relationships in socio-ecological networks?	Relating complexity and stability in socio-ecological networks
Response diversity	How do ecological interactions alter response diversity?	Assessing how different types of ecological interactions either homogenise or diversify responses across different ecosystems
	Do interactions across space determine the joint response of organisms?	Investigating spatial ecological networks and how interactions between habitats create similar or dissimilar responses
Ecological resilience	How does resilience vary across habitats, ecosystems and the globe?	Examining spatial interactions between ecological systems and their role in creating higher or lower levels of resilience at large scales
Eco-evolutionary processes	To what extent do co-evolutionary processes vary in space?	Investigating co-evolution across interacting groups of organisms (i.e. plants and pollinators) in different biogeographical regions
	Are we able to predict the role of an individual or species in a new biogeographical region based on its evolutionary history and ecological interactions?	Developing phylogenetically structured ecological networks across space to understand biogeographical variation in eco-evolutionary systems
Species distribution modelling	How can we directly integrate ecological interactions into SDMs?	Creating a framework to include positive and negative effects of different ecological interactions on species distribution and abundance
	What are the effects of both mutualistic and antagonistic interactions on species distributions?	Modelling the simultaneous effects of positive and negative ecological interactions on species distribution and abundance
Biogeography of ecological interactions	Should we use ecological interactions as biogeographical units?	Comparing biogeographical variation in species distributions, abundances and ecological interactions
Conservation	What are the most appropriate ecological network metrics or data to use for conservation?	Understanding how networks, and their commonly measured properties, link to conservation outcomes
	Can we identify keystone ecological interactions to conserve?	Assessing the importance of different ecological interactions in achieving conservation outcomes
	What methods provide the best option for setting conservation priorities over large spatial scales?	Comparing different methods in terms of their data demand, efficiency, accuracy and other important factors for decision-makers and conservationists
Restoration	How can restoration priorities be set at large spatial scales?	Investigating the use of spatial ecological networks can provide valuable information on restoration across sites
	Can we predict the effects of restoration activity?	Using eco-evolutionary methods to predict interactions and functional effects in ecosystems prior to restoration and validating the method with post-restoration monitoring Also see *Eco-evolutionary processes*
Global biomonitoring	Can we detect changes in ecological interactions across biogeographical scales?	Testing the sensitivity of ecological interaction change or turnover in comparison to other metrics (i.e. species richness)
	Can ecological interactions be used as an early warning signal for species' extinctions?	Examine historical datasets to investigate relationships between the loss of ecological interactions and secondary species extinctions in different ecosystems

shown that ecological interactions have biogeographical signatures (Albouy et al., 2019; Martins et al., 2021). We therefore suggest the occurrence and abundance of different ecological interactions or network structures could be used in a similar way to the occurrence and abundance of individual species or communities have been used to date.

A starting place to test the suitability of interaction data as biogeographical variables would be to focus on mutualistic interactions (e.g. plant–pollinators and plant–frugivores) as data are currently collected over large spatial scales, their dynamics are well understood, there is a standardised and comprehensive global taxonomy (Doré et al., 2021; McFadden et al., 2022), and they are directly linked to ecosystem service provision (Kremen, 2005). By combining species occurrence data with information on potential interactions using a metaweb (an ecological interaction network detailing all observed interactions for a group of organisms; see Gravel et al., 2019), it may be possible to generate more detail on ecological interactions at broad scales—that is, spatial variation in assembly, turnover and re-wiring (Redhead et al., 2018; Saravia et al., 2022). These data could then be implemented in decision-making frameworks through or-ganisations such as GEO BON (Walters & Scholes, 2017), supporting national and international monitoring strategies and environmental policy.

6 | IDENTIFYING CONSERVATION PRIORITIES BASED ON ECOLOGICAL NETWORKS

Conservation strategies focus on either iconic or keystone species, but often with relatively little or robust evidence demonstrating the wider importance of these organisms at different scales (Harvey et al., 2017). Ecological networks offer an exciting opportunity to determine species and locations of conservation priority based on either their ability to support a wider network of species, or the fact they are involved in key processes (i.e. keystone interactions responsible for specific ecosystem functions). Conservation based on ecological networks has been pointed to previously (Cumming et al., 2010), yet simply using summary statistics, which exclude information on the identity and strength of interactions and the conservation value of the species, does not provide a useful source of information for conservation decision-making (Heleno et al., 2012).

Leading on from the work of organisations such as the IUCN, it may be possible to use ecological interaction networks to inform global conservation. We suggest that ecological interactions and changes in structure over space and time should be used to detect signals within ecosystems that indicate threats to the environment. This work would build on conservation biogeography (Whittaker et al., 2005), but with a greater focus on species interactions, ecological networks and their role in generating ecosystem services. A focus should be placed on determining information that could be used to integrate ecological interaction networks into global conservation. For example, weighted generality or vulnerability could

indicate the susceptibility of different ecosystems to large preda-tor extinctions and therefore their relative conservation priority status.

Although a significant challenge, there are a number of options for setting continental and global conservation priorities using eco-logical networks: (i) identifying species and interactions that are disproportionately important for supporting (a) other species, (b) specific functions or processes or (c) robustness, stability and re-silience of the wider ecosystem (Márquez-Velásquez et al., 2021); (ii) detecting networks of habitats that can be used to maximise overall biodiversity and robustness to environmental change (Albert et al., 2017); (iii) determining local or regional hubs (nodes within a spatial network) that support either maximum species richness or ecosystem functions that could be targeted for conservation; and (iv) resolving the scale over which species' operate and interactions propagate (i.e. movement and dispersal networks) to identify the scale at which conservation priorities should be determined.

7 | USING INFORMATION ON ECOLOGICAL INTERACTIONS TO GUIDE RESTORATION

Ecological restoration has gained considerable attention given its potential to promote biodiversity and ecological functions at large scales (Strassburg et al., 2020). Ecological interactions can be used to support restoration ecology in several ways.

Restoration priorities can be informed by ecological interaction data. At large scales, important species or habitats (i.e. those involved in vital ecosystem functions) could be identified to target resto-ration efforts (also see Section 6). For example, Devoto et al. (2012) proposed and tested (in silico) two different pollinator restoration strategies, focusing on either functional complementarity or redun-dancy to identify important species at the landscape scale. Similar approaches could be applied with a spatial component, focusing on understanding how to restore the wider landscape through the promotion of ecological processes, such as seed dispersal (Silva et al., 2020). As a theoretical example, it would be possible to use network analyses to find species in plant–frugivore meta-networks (where seed dispersal can occur both within and between habitats) that can widely disperse seeds of favourable plants across the land-scape to facilitate restoration. Such information can also be used to make decisions on the best location for reintroductions—where ei-ther the environmental conditions or existing ecological interaction networks are optimal.

Ecological interaction networks can also be used to predict the effects of restoration, for example, species reintroductions (Baker et al., 2019). By understanding interaction networks in areas where a target species is either currently present (i.e. rem-nants of its current geographical range) or historically existed (i.e. historical records of ecological interactions), it may be pos-sible to predict effects in unsampled regions using phylogeneti-cally structured networks (Raimundo et al., 2018), trait-matching

(Pichler et al., 2020) and/or other methods that operate independently of species identities (which change across biogeographical space). As an example, in plant–frugivore networks large bodied organisms are able to disperse larger seeds, thus reintroducing large organisms to regions where they are extinct may contribute to the regeneration of plant communities (Mittelman et al., 2022).

8 | MONITORING THE EFFECTS OF GLOBAL ENVIRONMENTAL CHANGE

Changes in the distribution, abundance and extinction of species are commonly monitored at global scales. But as Daniel Janzen stated in his seminal 1974 essay 'The Deflowering of Central America' a more insidious and less easily observable form of extinction is the loss of ecological interactions (Janzen, 1974). Global biomonitoring, however, continues to miss this component of ecosystems, despite the fact that understanding changes in species interactions and differences in the structure across large spatial scales also allows for a mechanistic understanding of species loss and community responses to environmental change (Trøjelsgaard et al., 2015; Tylianakis & Morris, 2017). Even new metrics, such as the 'Essential Biodiversity Variables' (Pereira et al., 2013), have a restricted level of information regarding ecological interactions (Jetz et al., 2019). As a result, monitoring cannot suitably detect alterations in interactions prior to the complete extinction of a species. This means that a large amount of information on the beta-diversity of ecological interactions (i.e. spatial rewiring and turnover of interactions), and its increase or decrease, is not collected. Such information is vitally important with recent studies indicating substantial global scale changes in the identity of ecological interactions, with significant implications for ecosystem functioning. For example, research investigating plant–frugivore networks has shown that accelerating homogenisation of interactions across the globe is decreasing differences in interactions across continents (Fricke & Svenning, 2020), with other work showing that at ecoregion and biome scales species interactions form identifiable biogeographical boundaries that are sufficient to limit the propagation of disturbances across the globe (Martins et al., 2021). It is possible that we are losing a large number of functionally important ecological interactions across the globe without realising. This is problematic, not only due to the loss of ecosystem functions (Fricke et al., 2022), but also the subsequent impacts on the stability and resilience of ecological systems to future change (Petchey & Gaston, 2009; Valiente-Banuet et al., 2015).

By monitoring changes in species interactions at biogeographical scales, we may be able to predict and potentially prevent species extinctions, doing so is therefore of prime importance. Without a harmonised monitoring strategy that enables the integration of ecological interaction networks and other biomonitoring data, we cannot truly understand why biodiversity is responding in the way it is to global environmental change.

9 | FINAL REMARKS

Our understanding of global ecological patterns is increasing at an exponential rate, given emerging advances in monitoring and analysis. Approaches from network ecology offer a unique opportunity to investigate large-scale ecological patterns, and their mechanistic drivers, and as such have the capacity to advance various fields of research (Table 1). Here we have given examples of how we can use networks to understand, inform, conserve, restore and manage ecosystems in a way that allows for high levels of biodiversity and ecological functioning. We hope that this will motivate additional research to examine the forces shaping ecological networks as these emergent tools become increasingly integral to global land management efforts.

KEYWORDS
biodiversity, biomonitoring, conservation, ecological functioning, ecological interactions, macroecology, network ecology, restoration

CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
All data and code are available at https://github.com/hooge104/networks_connectance.

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