Comparing species interaction networks along environmental gradients

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ABSTRACT

Knowledge of species composition and their interactions, in the form of interaction networks, is required to understand processes shaping their distribution over time and space. As such, comparing ecological networks along environmental gradients represents a promising new research avenue to understand the organization of life. Variation in the position and intensity of links within networks along environmental gradients may be driven by turnover in species composition, by variation in species abundances and by abiotic influences on species interactions. While investigating changes in species composition has a long tradition, so far only a limited number of studies have examined changes in species interactions between networks, often with differing approaches. Here, we review studies investigating variation in network structures along environmental gradients, highlighting how methodological decisions about standardization can influence their conclusions. Due to their complexity, variation among ecological networks is frequently studied using properties that summarize the distribution or topology of interactions such as number of links, connectance, or modularity. These properties can either be compared directly or using a procedure of standardization. While measures of network structure can be directly related to changes along environmental gradients, standardization is frequently used to facilitate interpretation of variation in network properties by controlling for some co-variables, or *via* null models. Null models allow comparing the deviation of empirical networks from random expectations and are expected to provide a more mechanistic understanding of the factors shaping ecological networks when they are coupled with functional traits. As an illustration, we compare approaches to quantify the role of trait matching in driving the structure of

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plant–hummingbird mutualistic networks, i.e. a direct comparison, standardized by null models and hypothesis-based metaweb. Overall, our analysis warns against a comparison of studies that rely on distinct forms of standardization, as they are likely to highlight different signals. Fostering a better understanding of the analytical tools available and the signal they detect will help produce deeper insights into how and why ecological networks vary along environmental gradients.

Key words: network, metaweb, motif, rarefaction analysis, null model, environmental gradient, network comparison, network properties.

CONTENTS

I. INTRODUCTION

Ecological networks account for both species distributions and their interactions (Reiss *et al.*, 2009; Schleuning Fründ, & García, 2015) and provide an integrated representation of communities. They are, however, often considered as fixed entities isolated from one another, and are usually described at a single local site or region. Isolated networks are viewed as the result of deterministic ecological constraints (Clauset, Moore & Newman, 2008), such as forbidden links (Jordano, Bascompte & Olesen, 2003), functional composition (Gravel *et al.*, 2016), abundance (Vázquez & Aizen, 2004), morphology (Stang, Klinkhamer & van der Meijden, 2007; Rohr *et al.*, 2010) and phylogeny (Cattin *et al.*, 2004; Vázquez & Aizen, 2004; Brose, Williams & Martinez, 2006; Petchey *et al.*, 2008; Rohr *et al.*, 2010; Rohr & Bascompte, 2014). Variation of ecological networks in space or time is a novel and exciting approach to the analysis of community turnover. As shown in recent studies (Tylianakis *et al.*, 2008; Kissling *et al.*, 2012; Kissling & Schleuning, 2015; Schleuning *et al.*, 2015; Tylianakis & Morris, 2017), comparing ecological networks along environmental gradients can generate new

insights into the relative importance of environmental filtering and coexistence mechanisms behind community assembly. Beyond analysing general properties that are shared among ecological networks (Bascompte *et al.*, 2003), investigations of how networks vary along environmental gradients have the potential to provide insight into how abiotic conditions shape variation in species interactions.

Community ecology has predominantly focused on the structure of species assemblages within a single trophic level, such as plants (Weiher, Clarke & Keddy, 1998; Götzenberger *et al.*, 2012) or a guild such as bird communities (Diamond & Cody, 1975; Terborgh *et al.*, 1990). The description of assemblages not only by their co-occurrence but also by their interaction has nonetheless a long tradition, as pioneered by the work of Lindeman (1942), Odum (1956) and Margalef (1963). The idea that species are organized into interaction networks was proposed first for terrestrial ecosystems (e.g. plant–herbivore interactions; Elton, 1924) but was later developed mainly in marine ecosystems, e.g. intertidal marine organisms (Paine, 1966), mangroves (Odum & Heald, 1975) and coral reefs (Polovina, 1984). The development of this concept was slower for terrestrial systems and was only

recently established as a common approach for studying not just food webs, but also mutualistic (Pimm, 1991; Memmott, 1999; Dunne, Williams & Martinez, 2002; Olesen & Jordano, 2002; Bascompte *et al.*, 2003;) and host–parasite networks (Lafferty *et al.*, 2008). Empirical investigation of ecological networks requires documenting species presences, along with their interactions and environmental variables. Detection of these can be achieved through direct observation (e.g. records of flower visitors; Fabian *et al.*, 2013), use of video-camera systems (Maglianesi *et al.*, 2014; Weinstein, 2015), or by indirect methods such as removal experiments (Choler, Michalet & Callaway, 2001), quantification of gut contents (e.g. Barnes *et al.*, 2008), isotope analyses (e.g. Vander Zanden *et al.*, 1999) or molecular methods (e.g. García-Robledo *et al.*, 2013). To provide the most informative ecological signal, quantification of interactions should ideally go beyond the simple observation of the presence or absence of links, and instead estimate the strength of the interactions through time (e.g. interaction frequency between plants for hummingbirds). The documentation of ecological interactions has, however, been very resource-demanding, and only recently have approaches such as molecular barcoding (Jurado-Rivera *et al.*, 2009; González-Varo, Arroyo & Jordano, 2014), automated data collection using cameras or other technologies (Weinstein, 2015), as well as data-sharing (Martín González *et al.*, 2015; Poisot *et al.*, 2016) facilitated the study of ecological networks across sites and along environmental gradients (Wirta *et al.*, 2015).

Recent studies comparing the structure of ecological networks along environmental gradients have suggested that ecological and evolutionary constraints may shape networks differently in contrasting environments (Schleuning *et al.*, 2012; Hudson *et al.*, 2013; Layer, Hildrew & Woodward, 2013; Morris *et al.*, 2014; O'Gorman *et al.*, 2014; Martín González *et al.*, 2015; Osorio *et al.*, 2015). These studies highlighted how specific structural properties such as modularity, nestedness, or trophic specialization may vary under the shifting influences of processes such as environmental filtering, competition or facilitation (Layer *et al.*, 2010; Schleuning *et al.*, 2012; Martín González *et al.*, 2015; Cirtwill & Stouffer, 2016). For example, Martín González *et al.* (2015) showed that specialization in plant–hummingbird interaction networks is positively correlated with warmer temperatures and greater historical temperature stability. This can be interpreted as stronger competition for floral resources in warmer and more stable conditions, where specialization favours species co-existence.

Variation of ecological networks along environmental gradients may be driven by multiple factors, since the turnover of species and of interactions may be caused by several abiotic drivers (Poisot *et al.*, 2012). Our knowledge of how and why ecological networks vary along environmental gradients is still embryonic, despite increased interest in this field (Polis, Anderson & Holt, 1997; Warren, 1989; Dalsgaard *et al.*, 2011; Schleuning *et al.*, 2011). Part of this limitation is caused by the dearth of extensive interaction data sets. In addition, new methods are required to quantify recent networks that contain tens to hundreds of replicated networks (e.g. Krasnov *et al.*, 2004) or originate from reconstructed networks based on imposed rules (e.g. Albouy *et al.*, 2014). Finally, moving from understanding of 'how networks vary' to 'why networks vary' requires the development of new methodological approaches providing mechanistic insights rather than simple pattern detection (Beaumont, 2010; Gravel *et al.*, 2013, 2016).

Species turnover represents the most obvious source of variation of ecological networks along environmental gradients, as interactions between species are primarily conditioned by their co-occurrence (Gravel *et al.*, 2016). There are many drivers of species co-occurrence, such as environmental filtering, ecological interactions, dispersal limitations and historical contingencies (Peres-Neto, 2004; Pottier *et al.*, 2013). Abiotic conditions may also promote the turnover of interactions for given co-occurrences (Trøjelsgaard *et al.*, 2015). Variation in species abundance among sites may influence the frequency and detectability of interactions (Pellissier *et al.*, 2013; Bartomeus *et al.*, 2016) as more-abundant species are more likely to interact (Petchey, Brose & Rall, 2010; Canard *et al.*, 2014). Dominant morphologies or functional traits, for instance body size (Shin & Cury, 2001), both involved in trait-matching constraints (Gravel *et al.*, 2013; Albouy *et al.*, 2014; Bartomeus *et al.*, 2016; Hattab *et al.*, 2016), may also vary predictably with the environment (Shipley, Vile & Garnier, 2006). As an example, body size is larger in colder than in warmer conditions (Clarke & Warwick, 1999; O'Gorman *et al.*, 2016). Further complicating the picture, co-occurrence is required for an interaction to occur, but the interactions themselves may also affect co-occurrence (Cazelles *et al.*, 2016). For example, competitive interactions can potentially exclude a species from locations that would have otherwise favourable abiotic conditions (le le Roux *et al.*, 2012), or a predator could drive a prey toward an enemy-free location (Wisz *et al.*, 2013). When combined, these lines of evidence suggest that strong environmental clines should be associated with significant variation in the structure of ecological networks.

Comparing communities along environmental gradients has traditionally been used to gain a better understanding of how shifting ecological conditions shape the distinct structure of species assemblages, for instance species richness (e.g. Whittaker, Willis & Field, 2001; Macpherson, 2002), functional structure (Cornwell & Ackerly, 2009; Pellissier *et al.*, 2010; de Bello *et al.*, 2013), phylogenetic diversity (Graham *et al.*, 2009; Pellissier *et al.*, 2012) or multiple dimensions simultaneously (; Weinstein *et al.*, 2014; Dainese, Lepš & de Bello, 2015). Extending the species composition research agenda to ecological networks raises two new questions: what are the network properties to compare, and how to compare them? The first step in such analyses is to extract summary properties from different networks, such as nestedness (Dalsgaard *et al.*, 2013) or modularity (e.g. Morris *et al.*, 2014), which can be compared directly (Pouilly, Barrera & Rosales, 2006; Fabian *et al.*, 2013), or standardized to control for potential covariates (Bascompte *et al.*, 2003;

Aizen *et al.*, 2008; Schleuning *et al.*, 2011). Variation in network properties among sites is then interpreted in the light of distinct ecological processes (e.g. matching rules) reflecting different environmental pressures for the coexistence of species in communities (Pimm, 1991; Montoya, Pimm, & Sole, 2006). Blüthgen *et al.* (2008) argued that raw metrics, uncontrolled for neutrality or sampling effects, may be substantially flawed resulting in incorrect interpretation of variation across networks. Instead, properties describing network structure should be standardized but the most appropriate method to do so still requires discussion. Here, we review studies which have compared ecological networks along environmental gradients and present the most commonly applied methods with an emphasis on the standardization these methods employ. Using variation in plant–hummingbird mutualistic networks along an elevation gradient as a case study, we compare different methods and discuss their advantages and limitations, along with their ecological interpretation. Our review and case study show that the standardization employed can greatly influence the ecological interpretations of network variation along environmental gradients. We highlight the critical importance of methodological decisions, which should be aligned with the ecological hypotheses that are being tested.

II. SELECTING THE NETWORK PROPERTIES TO COMPARE

(1) α-properties

Studies of species diversity typically refer to the mean species diversity of a given site at a local scale as alpha diversity (α-diversity; Whittaker, 1972). By analogy, we here refer to α-properties as the characteristics of a local network. Some α-properties are strongly linked to the distribution of interactions such as species specialization or vulnerability (Schleuning *et al.*, 2011), while others are related to the topology of the network, including for example connectance (May, 1972; Jordano, 1987; Beckerman, Petchey & Warren, 2006; Santamaria & Rodriguez-Girones, 2007), centrality (Gonzalez *et al.*, 2010), nestedness (Bascompte *et al.*, 2003; Santamaria & Rodriguez-Girones, 2007), or modularity (Dalsgaard *et al.*, 2013). These properties can be directly extracted from the distribution and structure of nodes and links within each local ecological network. Moreover, the structure of ecological networks can be combined with complementary information, for example with phylogenies (Krasnov *et al.*, 2012; Pellissier *et al.*, 2013) or with functional traits (Maglianesi *et al.*, 2014) to compute more complex properties of networks. For example, Rezende *et al.* (2007) or Rohr & Bascompte (2014) combined phylogenies with ecological networks and showed a pervasive phylogenetic signal in the structure of species interactions. One may also use traits to compute more-specific metrics, such as ecological matching, when traits of one species should correspond to a trait syndrome of another to allow the

interaction (Maglianesi *et al.*, 2014; Weinstein & Graham, 2017). One major caveat of the computation of multiple network metrics is that they may show a strong degree of collinearity. Hence, the variation of one metric cannot be interpreted without either considering the variation of its correlate (Poisot & Gravel, 2014), building composite variables using multivariate approaches, or applying a form of standardization.

(2) β-properties

As a complement to the α-properties of ecological networks, β-properties quantify differences between pairs of networks or among multiple networks if a multiple-site dissimilarity measure is required to capture better the heterogeneity of sampled habitats and networks (Diserud & Odegaard, 2007; Melián *et al.*, 2015). Poisot *et al.* (2012) proposed quantification of the interactions in common between any pair of localities expressed over the total number of interactions. The total network dissimilarity is then divided into two components, one attributable to the turnover in species composition and the other to the turnover in interactions (Poisot *et al.*, 2012). The dissimilarity among ecological networks depends on both the change in the occurrence and the intensity of the interactions (Canard *et al.*, 2014). Using this approach, Trøjelsgaard *et al.* (2015) found that distant networks are more dissimilar to one another than closer ones, essentially because of spatial turnover in composition and abundances. As with α-properties, ecological networks can be coupled with species characteristics to compute functional β-properties, for example to quantify whether changes in ecological networks are associated with specific functional or phylogenetic modules. β-properties can be related to environmental differences among sites using a statistical model (e.g. Mantel test). While intuitive and intimately related to the long tradition of β-diversity analysis (Legendre, Borcard & Peres-Neto, 2005), this approach is only appropriate to compare ecological networks that share many species, whereas it might prove of limited use along environmental clines with significant species turnover. Moreover, the problem of co-varying factors is also relevant when relating β-properties to environmental differences among sites. Depending on the question, applying standardization to avoid biased interpretations can be necessary.

(3) Motif profiles

Ecological networks can be decomposed into smaller modules of interactions, such as omnivory, apparent competition, exploitative competition, and intra-guild predation (Leibold, 1995; Chase, 2003). Whenever these modules are overrepresented in a network, they are generally referred to as 'motifs' (Milo *et al.*, 2002). Motifs are hypothesized to be the building blocks of larger network structures (Bascompte & Melián, 2005; Stouffer *et al.*, 2007). Ecological networks can thus be described by the combination of all possible motifs of a given number of nodes found in a network (e.g.

there are 13 distinct possible motifs of three nodes). The frequency distribution of the different motifs will then reflect the signature of the network topology. This approach can point out conserved regions of the network, which can be key to their functioning under distinct environmental conditions (Baker *et al.*, 2015). Motif profiles have been related to certain aspects of community dynamics, such as coexistence and stability (Stouffer & Bascompte, 2011), and have been used to compare networks over space and time. For example, Baker *et al.* (2015) used this approach to investigate the spatial and temporal turnover of host–parasitoid interaction networks in southern Finland. They found that even though there is considerable turnover in species composition, the motif profiles are strongly conserved over spatial and temporal scales, suggesting a consistent network structure. While promising, the rationale of decomposing ecological networks in modules requires further evaluation with empirical data.

III. COMPARING ECOLOGICAL NETWORKS ALONG ENVIRONMENTAL GRADIENTS

(1) Comparing raw network properties

Ecological networks can be summarized by structural α- and β-properties, which include nestedness (Bascompte *et al.*, 2003), modularity (Olesen *et al.*, 2007), and turnover of interactions (Poisot *et al.*, 2012). These can be directly related to abiotic variables using various statistical approaches. For instance, Morris *et al.* (2014) evaluated whether connectance, modularity and other properties of antagonistic networks showed a latitudinal trend. After controlling for sampling effects (species diversity and size of the interaction matrix), they found no consistent latitudinal patterns in 216 quantitative networks of insect parasitoids. Because many network properties are intertwined with each other (Winemiller, 1989; Layer *et al.*, 2010), it is essential to control for a possible effect of co-variation, such as with species richness or relative abundance within a standardization procedure. Blüthgen *et al.* (2008) warned that the comparison of raw metrics may be substantially flawed, because of collinearity between network properties or due to underlying variation in species abundance or species richness (see Morris *et al.*, 2014). The same limitation applies to high-dimensional properties of network structures involving complementary sources of information such as traits and phylogenies (Rohr & Bascompte, 2014). For example, a direct comparison of the phylogenetic signal (e.g. through a correlation between phylogenetic distances and interactions) among networks only evaluates whether interactions are associated with the phylogenetic distance among species (Aizen *et al.*, 2016). Nevertheless, this direct comparison does not evaluate whether the same lineages interact with each other, nor identify the underlying ecological mechanism. A direct comparison of metrics is therefore expected to provide primarily a description of how different aspects of network structures vary along environmental gradients, but is less likely able to answer why they do so. Moreover, due to collinearity among metrics describing ecological networks, a direct comparison generally fails to disentangle the independent variation of a given property.

(2) Residual variation of network properties

The simplest approach to control for the co-variation of network properties is to use a linear regression to remove it and focus on the residuals thereof (e.g. Devoto, Medan & Montaldo, 2005; Tylianakis, Tscharntke & Lewis, 2007; Dalsgaard *et al.*, 2013; Trøjelsgaard *et al.*, 2013; Morris *et al.*, 2014). For example, connectance is a common metric for describing network complexity, but it is strongly correlated with species richness (Winemiller, 1990; Havens, 1992; Martinez, 1992), which constrains the potential arrangements of links (Poisot & Gravel, 2014). Quantifying the residual variation in connectance among sites that is independent of species richness provides a better measure of the degree of species association in an ecological network (Dunne *et al.*, 2002; Olesen & Jordano, 2002). In the situation of multiple collinear variables, structural equation models or path analyses are useful tools for disentangling the relative correlations of collinear variables along environmental gradients (Thébault & Fontaine, 2010). The study of residual variation provides the means to measure the variation of the property of ecological networks along environmental gradients independently of other co-variables. Although it still does not necessarily identify the underlying mechanisms, it allows us to quantify more precisely the variation of interest among ecological networks.

(3) Rarefaction analysis

Rarefaction techniques provide a way to compare ecological networks that differ in either sampling effort or community complexity across sites (Olesen *et al.*, 2011; Albrecht *et al.*, 2014; Morris *et al.*, 2014). In community ecology, rarefaction curves allow comparison between the observed or expected species richness in a relatively poorly sampled community with the expected species richness of a more extensively sampled community for an equivalent sampling effort, thereby removing confounding sampling effort effects (Simberloff, 1978; Gotelli & Colwell, 2001). In the context of ecological networks, rarefaction analyses allow the comparison of networks that differ in sampling effort, complexity, or species richness. Species and their associated interactions can be randomly removed from the most species-rich network to match the richness level of the species-poor network to which it is being compared. This operation can be repeated multiple times to obtain a statistical distribution of rarefied network properties (Albrecht *et al.*, 2014). The value of the property for the species-poor network can be compared to the distribution of the rarefied one. In Fig. 1, we illustrate this approach using 10 parasitic food webs in agricultural landscapes (Fabian *et al.*, 2013). Fig. 1 indicates that there is a positive correlation between difference in connectance and difference in the configuration
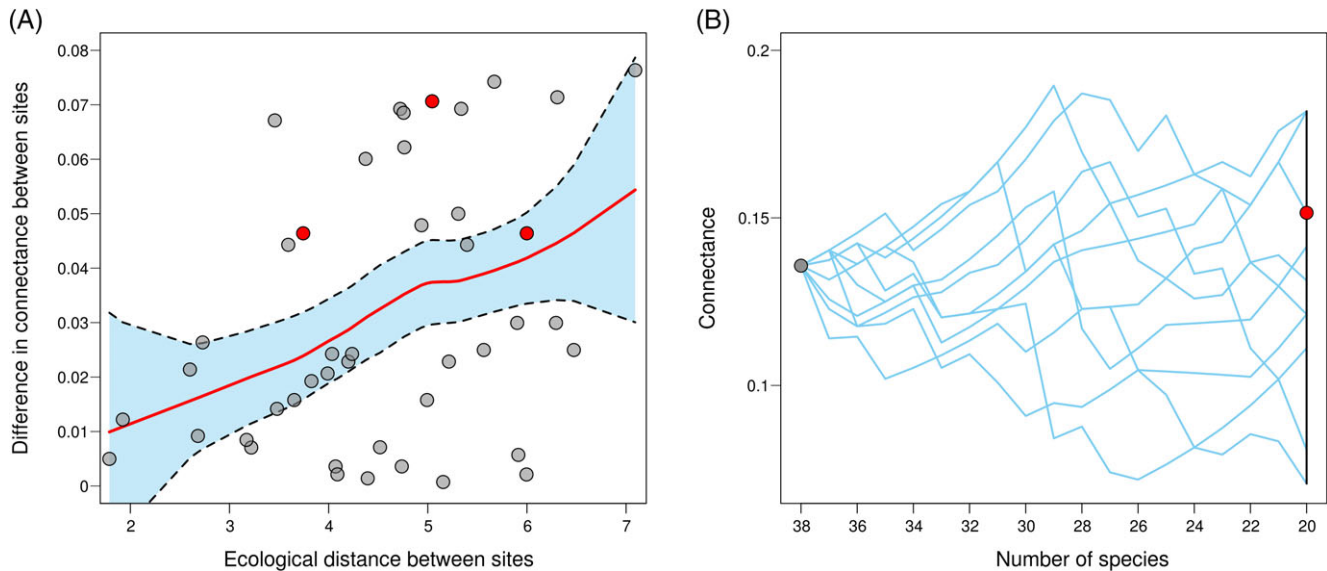
Fig. 1. Comparison of connectance of 10 hymenopteran food webs from Fabian *et al.* (2013) using the rarefaction method that removes species and links randomly. (A) Relation between ecological distance and difference in connectance between sites. The ecological distance between sites was expressed as the Euclidean distance between the percentage cover by six landscape elements on the different sites: (*i*) agricultural fields; (*ii*) extensive meadows, gardens, orchards and hedges; (*iii*) forest; (*iv*) wildflower strips; (*v*) water bodies and (*vi*) urban areas (roads and houses). Red dots on the graph identify the only three pairs of networks that showed a significant difference in connectance when values were compared after rarefaction. The red line is a local polynomial regression fitted with a confidence interval of 95% (shaded blue). (B) The observed connectance of the smallest network (red dot; 20 species) compared with the distribution of rarefied connectance with 10 iterations from a richer species network (38 species). In this example, the two measures of connectance are not different.

of the agricultural landscape among sites, which is, however, confounded by underlying variation in species richness. When accounting for differences in species richness using a rarefaction approach, only three pairs of sites at similar richness level showed significant differences in connectance. The overall gradient in connectance needs to be robust to differences in species richness before conclusions can be drawn about apparent underlying differences in connectance per site.

(4) Null models

Null models are useful for evaluating whether a specific structural property may be the result of chance alone in the absence of any particular ecological constraint (Gotelli & Graves, 1996; Gotelli, 2001). This approach has been used widely in spatial community ecology to evaluate whether community structure, such as the distribution of abundance or functional dispersion, differs from random sampling of the regional species pool (Götzenberger *et al.*, 2012). Null models are also applied to the analysis of ecological networks (Bascompte *et al.*, 2003; Ollerton *et al.*, 2007) and along environmental gradients (see Table 1). Here, the value of the network property of interest is contrasted to expected values from the null models, where the links within each network are randomized. The randomization might be constrained, e.g. by fixing the species' relative abundances. Blüthgen *et al.* (2008) showed that the deviation of network properties from null expectations varies according to the relative abundance

of the species. If partners associate randomly, species are more likely to interact with common than with rare partners. Since species abundances and frequencies are known to co-vary with environmental gradients (Lomolino, 2001), a null model accounting for the abundance or frequency of species provides a more relevant baseline to highlight changes in species interactions along the gradient (Schleuning *et al.*, 2012; Sebastián-González *et al.*, 2015).

Null models have also been used to evaluate the role of functional traits in structuring ecological networks. Trait matching between mutualistic or antagonistic partners is compared to the values expected when the association of species with their traits is randomized. Null models have been used for the evaluation, for example, of whether the functional matching of interactions is stricter than expected under random associations (Fig. 2B). The standard effect size (SES) – the difference of the observation relative to the null distribution – is related to environmental gradients using a statistical model (Schleuning *et al.*, 2012). As emphasized by de Bello *et al.* (2013), null models are not 'magic wands', and a linear dependence between the SES and the original raw metric is frequently observed. Similarly, it is not known whether standardized measures generated by null models can be properly compared across networks with different dimensions. The architecture of a null model requires careful evaluation (e.g. using simulated data) to understand clearly whether the confounding effects are attenuated as anticipated.

Table 1. Publications where mutualistic or antagonistic ecological networks were compared along environmental gradients, together with the summary network property considered, the environmental gradient, and the standardization approach used. Comparing ecological networks along environmental gradients is an emerging field; most of the 25 studies listed here use either a residual analysis or null models to standardize the comparison.

Network type	Property	Ecological gradient	Method	Reference	Title
Antagonistic	Species richness, trophic composition	Elevation	Comparing raw properties	Pouilly et al. (2006)	Changes of taxonomic and trophic structure of fish assemblages along an environmental gradient in the Upper Beni watershed (Bolivia)
Mutualistic	Specialization	Latitude, past and contemporary climate, plant diversity	Null model	Schleuning et al. (2012)	Specialization of mutualistic interaction networks towards tropical latitudes
Antagonistic	Rates of parasitism, linkage density, generality, vulnerability, evenness, connectance, compartment diversity	Habitat modification	Adding a statistical cofactor	Tylianakis et al. (2007)	Habitat modification alters the structure of tropical host–parasitoid food webs
Mutualistic	Specialization, connectance, number of interactions	Precipitation, elevation	Adding a statistical cofactor	Devoto et al. (2005)	Patterns of interaction between plants and pollinators along an environmental gradient
Mutualistic	Connectance, nestedness, degree of distribution, modularity	Elevation	Null model	Ramos-Jiliberto et al. (2010)	Topological change of Andean plant–pollinator networks along an altitudinal gradient
Mutualistic	Modularity and nestedness	Historical and contemporary climate change	Comparing raw properties	Dalsgaard et al. (2013)	Historical climate change influences modularity and nestedness of pollination networks
Mutualistic	Modularity and nestedness	Latitude, elevation, temperature, precipitation	Null model	Trøjelsgaard et al. (2013)	Macroecology of pollination networks
Mutualistic	Specialization	Elevation, historical climate change (velocity), contemporary climate change (precipitation, temperature), species richness and seasonality	Null model	Dalsgaard et al. (2011)	Specialization in plant–hummingbird networks is associated with species richness, contemporary precipitation and quaternary climate-change velocity
Mutualistic	Modularity and nestedness	Latitude, climate, topography, human impact	Null model	Sebastián-González et al. (2015)	Macroecological trends in nestedness and modularity of seed-dispersal networks: human impact matters
Antagonistic	Trophic level and contribution of benthic carbon to diet	Inshore–offshore	Comparing raw properties	Kopp et al. (2015)	Reorganization of a marine trophic network along an inshore–offshore gradient due to stronger pelagic–benthic coupling in coastal areas
Antagonistic & mutualistic	Modularity and nestedness	Temperature, precipitation	Adding a statistical cofactor	Welti & Joern (2015)	Structure of trophic and mutualistic networks across broad environmental gradients
Antagonistic	Trophic levels, connectance, generality, vulnerability	Estuarine–costal	Niche model	Vinagre & Costa (2014)	Estuarine–coastal gradient in food-web network structure and properties
Antagonistic	Linkage density, connectance, generality, vulnerability, modularity, specialization	Latitude	Comparing raw properties	Morris et al. (2014)	Antagonistic interaction networks are structured independently of latitude and host guild
Antagonistic	Generality, vulnerability, connectance, interaction evenness	Elevation	Adding a statistical cofactor	Maunsell et al. (2015)	Changes in host–parasitoid food web structure with elevation

Table 1. Continued

| Network type	Property	Ecological gradient	Reference	Method	Title
Mutualistic	Number of compartments, modularity, number of modules, nestedness, connectance, pollinator:plant ratio, robustness	Invasion status	Albrecht et al. (2014)	Rarefaction analysis	Consequences of plant invasions on compartmentalization and species' roles in plant–pollinator networks
Antagonistic	Species composition and species interaction	Temperature, isothermality, precipitation, diurnal range	Poisot et al. (2016)	Beta-diversity	Hosts, parasites, and their interactions respond to different climatic variables
Antagonistic	Herbivore and predator biomass, and herbivore composition	Productivity	Chase (2003)	Comparing raw properties	Strong and weak trophic cascades along a productivity gradient
Antagonistic	Phenotypic and ecological specialization	Elevation	Maglianesi et al. (2014)	Comparing raw properties	The role of morphological traits (i.e. phenotypic specialization) for ecological specialization in plant–hummingbird networks in three types of Neotropical forests at different elevations
Antagonistic	Mean species richness, total community abundance, functional group abundance, extinction frequency, and temporal variability in abundance	Latitude	Tuck & Romanuk (2012)	Comparing raw properties	Robustness to thermal variability differs along a latitudinal gradient in zooplankton communities
Antagonistic	Link, chain, omnivory properties	Altitude (river gradient)	Romanuk et al. (2006)	Comparing raw properties	The structure of food webs along river networks
Antagonistic	Trophic groups, linkage density, connectance, generality, vulnerability, trophic path length	Human impact	Coll et al. (2011)	Comparing raw properties	Food-web structure of seagrass communities across different spatial scales and human impacts
Antagonistic	Specialization	Latitude	Dalsgaard et al. (2017)	Null model	Opposed latitudinal patterns of network-derived and dietary specialization in avian plant–frugivore interaction systems
Mutualistic	Specialization	Latitude	Pauw & Stanway (2015)	Null model	Unrivalled specialization in a pollination network from South Africa reveals that specialization increases with latitude only in the Southern Hemisphere
Antagonistic	Mass ratios between trophic levels	Latitude	Romero et al. (2016)	Comparing raw properties	Food-web structure shaped by habitat size and climate across a latitudinal gradient
Antagonistic	Vulnerability, generality, link density, interaction diversity, compartment diversity	Landscape composition	Fabian et al. (2013)	Comparing raw properties	Importance of landscape and spatial structure for hymenopteran-based food webs in an agro-ecosystem
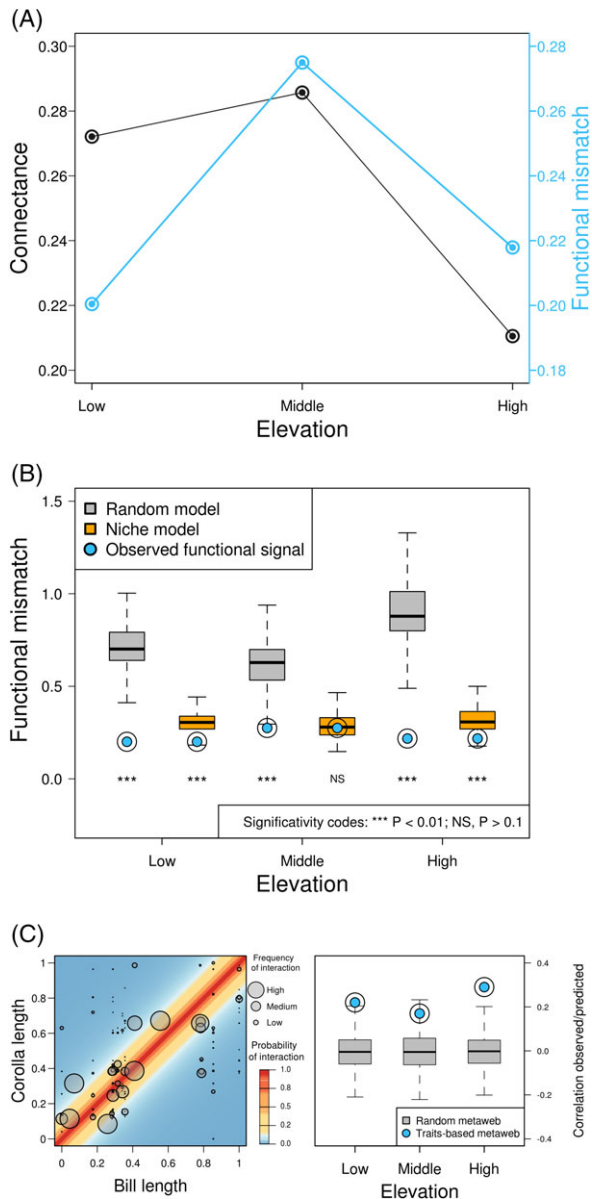
Fig. 2. Methods to compare ecological networks illustrated for the case study of plant–hummingbird mutualistic networks along an elevation gradient in Costa Rica: wet forest (50 m; 10°26′N, 84°01′W), pre-montane forest (1000 m; 10°16′N, 84°05′W), and lower montane wet forest (2000 m; 10°11′N, 84°07′W). For further details about the study site, see Maglianesi *et al.* (2014). (A) Connectance and functional mismatch (measured as the mean absolute difference between bill and flower corolla length) *versus* elevation. (B) Observed functional matching compared to two null models: randomized 999 times within each local network (grey) and the niche model of species interaction (orange; Williams & Martinez, 2000). The black line represents the median, the upper and lower limits of the box are the first and third quartile, respectively, and the whiskers represent 1.5 times the distance between the first and third quartiles. (C) Correlation between the observed interaction frequencies and those expected from a metaweb assuming the highest frequency of interaction for species with matching bill and corolla standardized length.

(5) Comparison to a hypothesis-based metaweb

The metaweb represents potential interactions among all species from the regional pool (Dunne, 2006) and provides an alternative approach to compare the structure of ecological networks. Instead of assembling each local ecological network by randomly drawing from the overall interaction pool, as is generally done with null models (Schleuning *et al.*, 2012; Sebastián-González *et al.*, 2015), one can generate a network of expected interactions between all the species in the regional pool under specific constraints (Havens, 1992). The architecture of a metaweb can be based on pure random interactions, which would correspond to a regional random null model, or can further account for the species frequency distribution in the species pool, trait matching (Morales-Castilla *et al.*, 2015; Bartomeus *et al.*, 2016), or phylogenetic relatedness (Pellissier *et al.*, 2013). The deviation of local networks from the metaweb can both inform whether the latter provides a sufficient approximation of realized networks or whether some local structure deviates more than others in particular parts of the environmental gradient. We illustrate in Fig. 3 different metawebs of trophic interactions among Mediterranean fish species built from species co-occurrence, trait or phylogenetic matching. We show that a Mediterranean metaweb built using body size provides a better fit to the local network in the Gulf of Gabes, a southern Mediterranean ecosystem along the Tunisian coast. In this example, only one local network is compared to the metaweb, but this analysis can be extended to an entire gradient (e.g. of bathymetry) and used to determine if there are locations where the body size relationship is not sufficient to explain the network complexity. Deviation of local ecological networks from the metaweb can be quantified using, for example, the True Skill Statistic (TSS; Allouche, Tsoar & Kadmon, 2006) for binary interactions (Fig. 3) or a correlation for quantitative links (Fig. 2C) and thus related to environmental gradients. For instance, Gravel *et al.* (2011) investigated 50 trophic networks in Canadian lakes and found that the structure of many local networks was different from that expected under a random metaweb, with much greater connectance and generality on average than the null expectation. This approach is adjustable to the hypotheses serving to create the metaweb, so that environment-specific deviations from expected rules (e.g. random, abundance-based, and trait-matching) can be quantified. This approach necessitates that the anticipated metaweb is based on ecologically sound assumptions, and will thus require some prior knowledge of the system.

(6) Network alignment

The alignments of the motifs within networks have been argued to provide a flexible approach to detect whether networks have a common core structure along environmental gradients (Morales-Castilla *et al.*, 2015). Alignment may be used to match motifs composed of several nodes among different networks. Conceptually, the method has some similarities with the alignment of sequences of nucleotides
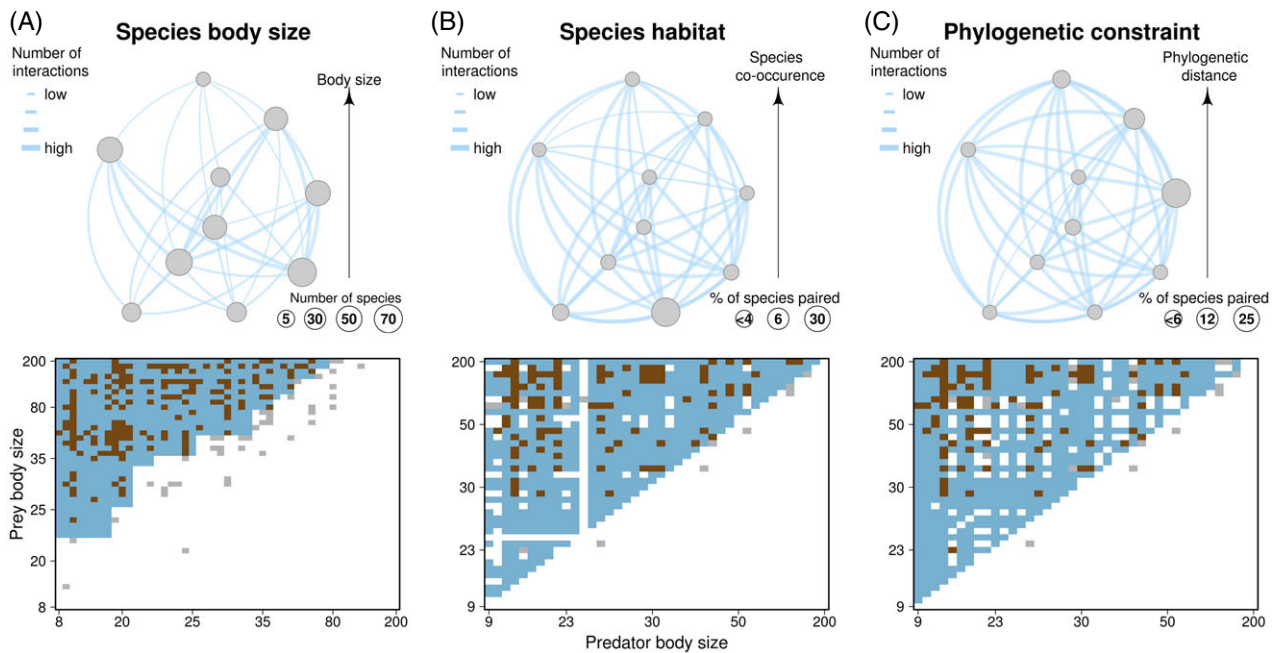
Fig. 3. Hypothesis-based metaweb of fish from the Mediterranean Sea. Upper images show three contrasting hypothesis-based metawebs, based on (A) body size data from Barnes *et al.* (2008), (B) habitat preferences (e.g. benthic, pelagic; Albouy *et al.*, 2015) and (C) phylogenetic distance between groups of co-occurring species based on the phylogeny of Mediterranean fish in Meynard *et al.* (2012). Lower images show metaweb expectations compared to the observed food web for the Gulf of Gabes on the Tunisian coast (Hattab *et al.*, 2016). The grey colour on the graph represents the observed values, blue represents the expected values according to the hypothesis, and brown is the match between the expected and observed values. The body size hypothesis showed the strongest association to the observed Gabes food web with the highest True Skill Statistic (TSS) values (TSS$_{size}$ = 0.55, TSS$_{habitat}$ = 0.5, TSS$_{phylo}$ = 0.44). This comparison can be applied to any food web across the Mediterranean Sea.

performed to compute phylogenies, as it needs to maximize the motif match among networks using a cost function. The cost function could be simple (e.g. by looking at the fraction of matched interactions for each pair of nodes) or use a finer description of the topology. For instance, Stouffer *et al.* (2012) computed the motif profile for each node, i.e. the frequency at which a node belongs to a set of motifs – also called species role – and computed the average correlation between the profiles of pairs of nodes. This approach can be extended to evaluate the recurrence of common motifs across networks in distinct environments and can identify which conserved regions of the network are key to its functioning (Baker *et al.*, 2015). This approach enables us to quantify the similarity of the topology between very different pairs of ecological networks, even those with no species in common, such as between marine and terrestrial systems. However, it still requires further development to become a standard tool for network comparison along environmental gradients.

(7) Statistical model coupling co-occurrence with interactions

The dissimilarity among ecological networks along environmental gradients can be decomposed using a set of statistical models for species distributions and their interactions (Gravel *et al.*, 2016). Models of co-occurrence or co-variation in abundance, so called joint species distribution models, have

been developed over the last decade (Pollock *et al.*, 2014; Warton *et al.*, 2015; Ovaskainen *et al.*, 2017). These joint species distribution models predict species distributions based on environmental and spatial variables and allow sharing of information on species distribution and thereby improve the estimation of parameters. Statistical models might not only integrate co-occurrence, but also the interactions that link species to each other to account better for the way abiotic and biotic factors interact with each other to shape species assemblages along environmental gradients (Cazelles *et al.*, 2016). For instance, Gravel *et al.* (2016) combined a co-occurrence model with a trait-matching model, both interacting with climatic variations, to understand more mechanistically the drivers of interaction turnover in plant–herbivore networks. The main limitation of this approach, however, is that it requires a large amount of replicated records of interactions along environmental gradients for calibration and to perform a suitable evaluation of the model parameters, including the interaction between abiotic and biotic effects.

IV. WHAT IS THE BEST APPROACH FOR COMPARING ECOLOGICAL NETWORKS?

Studies comparing ecological networks along environmental gradients are relatively scarce in contrast to more traditional

community analyses looking at species richness or functional traits within a single trophic level. We reviewed 25 studies (Table 1) that compared ecological networks along a variety of gradients, including elevation (Devoto *et al.*, 2005; Ramos-Jiliberto *et al.*, 2010; Maunsell *et al.*, 2015) and latitude (Sebastián-González *et al.*, 2015). This limited number of studies contrasts with the hundreds of publications in community ecology (Götzenberger *et al.*, 2012). The use of residual correlations and null models were the most common approaches to standardize and compare ecological networks along environmental gradients. Only one study used a metaweb (Gravel *et al.*, 2011) or a full species co-occurrence–interaction coupled model (Gravel *et al.*, 2016) to evaluate the role of the abiotic environment in shaping ecological networks. Moreover, most studies compared summary properties based on the distribution of links and network topologies along environmental gradients, and generally did not include functional traits. Researchers investigating the structure of ecological networks along gradients should agree on the most appropriate approach(es) given a data set, and ponder the nature of the variation – and its ecological interpretation – that is quantified.

(1) The plant–hummingbird case study

Here, we compare direct and standardized quantification of the structure of ecological networks using a data set of plant–hummingbird mutualistic interactions along an elevation gradient in Costa Rica. Maglianesi *et al.* (2014) recorded plant visitation by hummingbirds over a year at three different elevations in Costa Rica and constructed quantitative networks of interaction frequencies. Observations of interactions between plant and hummingbird species in the understorey were carried out using videotaping of flowers. Tracked individual plants were randomly selected for each species at each study site. To record visits of hummingbirds to individual plants, unattended cameras were fixed 10 m from open flowers for periods of 120 min between 06:00 and 14:00 h. Morphological traits for hummingbirds and plants were measured, including bill length and corolla length, which are expected to drive interactions in this type of network (Maglianesi *et al.*, 2014).

(2) Comparison of plant–hummingbird network properties

We compared the connectance along elevation to exemplify the direct use of a summary metric. We found that connectance decreased with elevation (Fig. 2A), while species richness was constant (low elevation network 28 species; medium elevation network 26 species; high elevation network 28 species). Connectance is a topological measure, representing the ratio of realized links over potential links. Even though they present the same species richness, the configuration of the three networks is different (e.g. 7 bird species and 21 plant species at low elevation; 9 bird species and 19 plant species at high elevation). The shape

of the interaction matrices (lines × columns) constrains the number of potential links and the connectance within each network. The variation in connectance may be due to environmental filtering acting on species co-occurrence or a change in how species interact, but a direct comparison of connectance provides limited information on those processes. We therefore combined ecological networks with species functional traits and evaluated the role of trait matching in constraining these interactions. We quantified the absolute mean difference between species bill and corolla length for each observed interaction. This unstandardized measure of functional mismatch was lowest for the low elevation sites, peaked at the middle elevation site and was low again in the highest elevation site (Fig. 2A). Using a direct approach, it remains unclear whether the trait-matching constraint changes over the gradient, or is driven by underlying changes in species functional traits in the species pool.

(3) Comparison of trait matching with two null models

We next compared observed trait matching to two different null expectations, a model where the frequencies of interactions were randomized within each network and the niche model of food-web structure (Williams & Martinez, 2000). Compared to the random null model, all the observed trait matches were significantly lower than random, suggesting that the observed matching cannot be generated by a random distribution of the interactions within each network (Fig. 2B). The use of the niche model as a null hypothesis, as in Dunne, Williams & Martinez (2004), provides more conservative results, with the middle-elevation site not different from the null model. These results suggest that the partitioning of interactions between hummingbirds and plants along a directional niche axis (defined with a centroid and a range) is sufficient to explain the structure of the middle-elevation site, while the other methods suggest a more complex structure. In these cases, the centroid and range of the empirical networks are not random, and show more pronounced niche partitioning due to traits. Hence, the selection of the appropriate null model, either straight randomization (Schleuning *et al.*, 2012), or the niche model (Dunne *et al.*, 2004), should be explicitly justified and its hypothesis clearly established.

(4) The use of hypothesis-based metaweb

We built hypothesis-based metawebs to which local ecological networks can be compared. We constructed a metaweb assuming perfect matching between bill and flower length (Maglianesi *et al.*, 2014). With this hypothesis, interactions are expected to be more frequent near the 1:1 line of a matrix, in which hummingbird bill and plant corolla are ordered by size. The middle-elevation site is slightly lower, but all sites conform moderately well to the metaweb-based hypothesis of functional matching, with the highest elevation showing the best match (Fig. 2C). For comparison, we generated a set of 999 random metawebs and extracted

from each three local webs. We tested whether similar levels of correlation between the observed and modelled interaction arose from random regional metawebs. As found with the randomization performed within each network using the null-model approach, the correlation from a subset of the functional metaweb was higher than from a subset of a random regional metaweb. This indicates that all three networks are more consistent with functional matching than random assembly.

(5) Conclusions from the plant–hummingbird networks

Together, the direct (Fig. 2A, B) and the standardized approaches (Fig. 2C) provide different insights into how and why the structure of plant–hummingbird ecological networks varies along this elevation gradient. Scoring of sites in terms of intensity of matching differed in a direct comparison of the matching values (mean difference between species bill and corolla length in mm: low = 0.2, middle = 0.27, high = 0.22; Fig. 2A), the random null model (SES: low = −4.37, middle = −3.9, high = −3.5; Fig. 2B), the niche model (SES: low = −2.58, middle = −1.28, high = −2.9; Fig. 2B) and after a standardization with a metaweb (correlation to the functional metaweb: low = 0.22, middle = 0.17, high = 0.29; Fig. 2C). While the SES of the null model decreased with increasing elevation, the ranking of SES for the niche model showed a different order, with the greatest value in the high-elevation site. Finally, the highest elevation site also provided a better match for the hypothesis of trait matching as evidenced by the metaweb comparison. Although the plant–hummingbird case provides a first caution regarding the importance of methodological choice in a comparison of ecological networks, evaluating a greater variety of networks (e.g. antagonistic) across different environmental gradients and with different methods is needed. Our illustration calls for a careful selection of appropriate methods according to prior hypotheses, since the selection of the method will essentially determine the variation being analysed.

V. CONCLUSIONS

(1) There is a limited number of investigations of ecological network variation along environmental gradients because of the difficulty of quantifying interactions among species. Nevertheless, we expect that the rise of molecular techniques will allow better and faster quantification of ecological networks (Pompanon et al., 2012; Roslin & Majaneva, 2016; Vacher et al., 2016), allowing more spatial replication along environmental gradients. Moreover, the use of automated recording systems (Weinstein, 2015; Bohan et al., 2017) is also expected to expedite the collection of interaction data compared with manual techniques.

(2) Species information such as functional traits should be collected together with interactions in order to reach a good ecological understanding of why ecological networks vary along gradients. Alternatively, trait data might be gathered from available databases in isolation from the interaction, but the resulting analyses would not be able to highlight intraspecific co-variation between phenotypic traits and network structure along environmental gradients. When trait data are unavailable, a comparison of ecological networks along environmental gradients is limited to approaches that do not rely on functional traits (e.g. Dalsgaard et al., 2013; Sebastián-González et al., 2015), but that might provide more limited ecological inferences.

(3) Several approaches have been used to compare ecological networks either by analysing raw properties or using forms of standardization. Our review and case study suggest that different approaches are not directly comparable, and that this precludes, for the present, any meta-analysis of network variation along multiple gradients. Beyond analytical results, we call for further efforts to facilitate the exchange of raw data of species interaction networks along environmental gradients [e.g. MANGAL (Poisot et al., 2016), 'Interactionweb' or 'Web of Life']. Finally, studies comparing different approaches using empirical (e.g. bipartite antagonistic or mutualistic networks, food webs) or simulated data sets and discussing methodological bias are critical to provide guidance to select an appropriate methodology when comparing ecological networks.

(4) We stress the need to agree on the most appropriate methodology to compare ecological networks along environmental gradients – on the one hand, when only data on network structure are available, and on the other when functional traits are also available. It is unlikely that one methodology can be used to answer all possible questions and future research should focus on understanding links between the different methodologies and the questions that they may answer.

Entwicklung Wissenschaftlich-o¨ konomischer Exzellenz" of Hesse's Ministry of Higher Education, Research, and the Arts.

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