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Predicting ecosystem functions from biodiversity and mutualistic networks: an extension of trait-based concepts to plant–animal interactions

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Research linking biodiversity and ecosystem functioning (BEF) has been mostly centred on the influence of species richness on ecosystem functions in small-scale experiments with single trophic levels. In natural ecosystems, many ecosystem functions are mediated by interactions between plants and animals, such as pollination and seed dispersal by animals, for which BEF relationships are little understood. Largely disconnected from BEF research, network ecology has examined the structural diversity of complex ecological networks of interacting species. Here, we provide an overview of the most important concepts in BEF and ecological network research and exemplify their applicability to natural ecosystems with examples from pollination and seed-dispersal studies. In a synthesis, we connect the structural approaches of network analysis with the trait-based approaches of BEF research and propose a conceptual trait-based model for understanding BEF relationships of plant–animal interactions in natural ecosystems. The model describes the sequential processes that determine the BEF relationship, i.e. the responses of species to environmental filters, the matching of species in ecological networks and the functionality of species in terms of their quantitative and qualitative contributions to plant demography and ecosystem functioning. We illustrate this conceptual integration with examples from mutualistic interactions and highlight its value for predicting the consequences of biodiversity loss for multispecies interactions and ecosystem functions. We foresee that a better integration between BEF and network research will improve our mechanistic understanding of how biodiversity relates to the functioning of natural ecosystems. Our conceptual model is a step towards this integration between structural and functional biodiversity research.

Interactions between organisms, species and trophic levels are the backbone of biodiversity (Bascompte and Jordano 2007) and ecosystem functioning (Loreau 2010). Mutualistic interactions, for instance between plants and pollinators or seed dispersers, influence the structure, stability and functioning of ecological communities (Kremen et al. 2007). The fate of these multispecies interactions in a changing world and the ecosystem consequences of disrupting their diversity have become important research topics during the last decade (Kremen et al. 2007, Reiss et al. 2009, Díaz et al. 2013). Despite much research on the relationship between biodiversity and ecosystem functioning (BEF), this relationship is still little understood for mutualistic plant–animal interactions.

In this review and synthesis paper, we address the importance of biodiversity and plant–animal mutualistic interactions for ecosystem functioning from two angles. First, we summarize advances in BEF research and exemplify BEF relationships for mutualistic interactions, specifically for pollination and seed dispersal by animals. Second, we introduce concepts that describe the structural diversity of

plant–animal mutualistic networks in natural ecosystems. In the third section, we connect the structural approaches of network theory with the trait-based approaches of BEF research and thereby integrate structural and functional approaches of biodiversity research in a coherent framework. We exemplify the usefulness of this framework with examples from mutualistic interactions and highlight its value for predicting the consequences of biodiversity loss for multispecies interactions and ecosystem functions.

Biodiversity and ecosystem functioning (BEF)

Plant–pollinator and plant–seed disperser mutualistic interactions determine two distinct processes in the life cycle of plants: pollination and seed dispersal. Both processes affect plant demography and at the ecosystem level influence vegetation dynamics (Kremen et al. 2007, Díaz et al. 2013). Hence, both processes contribute to ecosystem functioning through biological activity and are defined as ecosystem

processes or functions (sensu Reiss et al. 2009). The outcomes of both functions may directly or indirectly benefit human endeavours, for instance by promoting crop yield or forest restoration (Kremen 2005), and in such cases pollination and seed dispersal are also ecosystem services (sensu Hooper et al. 2005).

The assessment of pollination and seed-dispersal functions requires the distinction between their quantitative and qualitative components (Herrera 1987, Schupp et al. 2010). The quantitative component of pollination and seed dispersal depends on the frequency of interactions between animals and plants (e.g. the number of flowers visited by a pollinator or the number of seeds removed by a disperser) and should be closely related to the abundance of plant and animal species (Herrera 1989, Jordano and Schupp 2000). The qualitative component represents the qualitative differences among animal species in their ultimate effect on plant fitness, irrespective of their interaction frequencies (e.g. the quality of pollen grains deposited on the flowers or the suitability of seed-deposition sites for germination). Pollination and seed-dispersal qualities depend on animal traits and behaviour (e.g. big pollinators with large home ranges deposit a higher proportion of outcross pollen, Ne'eman et al. 2010), the interaction between animal traits and environmental conditions (e.g. big dispersers deliver many seeds at usually less hostile sites at long distances from source plants, McConkey and Brockelman 2011) and interspecific interactions between mutualists (e.g. competition among pollinators increases floral fidelity and conspecific pollen deposition, Brosi and Briggs 2013). Quantitative and qualitative components may be integrated through the concept of effectiveness that defines the functional importance of a mutualist by the product of its quantitative and qualitative contributions to the respective ecosystem function (Herrera 1987, Ne'eman et al. 2010, Schupp et al. 2010). For example, the most effective and functionally most important seed disperser would be an animal moving many seeds of a plant species to a habitat patch suitable for seedling establishment.

BEF relationships for pollination and seed-dispersal interactions

There is principal consensus on the idea that richer biota are able to accumulate more biomass, use resources more efficiently and resist better to disturbance than communities impoverished by species' extinction (Loreau et al. 2001, Hooper et al. 2005). BEF relationships have mostly emerged from controlled, short-term and small-scale experiments focusing on single trophic levels and productivity-based functions (e.g. plant biomass, Balvanera et al. 2006). More recent experimental work has widened BEF relationships to food webs and other multitrophic interactions (Reiss et al. 2009, Scherber et al. 2010, Thompson et al. 2012). However, knowledge on the responses of cross-trophic ecosystem functions to biodiversity change is still vague, especially at large spatiotemporal scales in natural ecosystems (Ives et al. 2005, Duffy 2009, Peh and Lewis 2012). Observational studies of pollinator and seed-disperser assemblages along land-use gradients found an increase in pollination and seed-dispersal functions with an increasing richness of pollinators (Kremen

et al. 2002, Klein et al. 2003, Hoehn et al. 2008) and seed dispersers (Pejchar et al. 2008, García and Martínez 2012). Similar patterns have emerged from experimental, small-scale studies manipulating pollinator richness (Fontaine et al. 2006, Albrecht et al. 2012, Fründ et al. 2013). Richness effects have been found on both quantitative and qualitative components of pollination and seed-dispersal functions (García and Martínez 2012, Fründ et al. 2013).

Mechanisms of BEF relationships

Three main mechanisms could explain an increasing performance of pollination and seed-dispersal functions with an increasing richness of animal mutualists: sampling effects, complementarity and interspecific interactions (Fig. 1). Sampling effects (also dominance/selection effects, Loreau et al. 2001) derive from the increased probability of adding a dominant species (i.e. a key provider of a particular ecosystem function, Ives et al. 2005) when randomly adding species to an assemblage (Fig. 1A). In a pollinator-richness experiment, single social bee species enhanced plant seed set, due to their high visitation rates (Albrecht et al. 2012). A dominance effect of a particular bird species was the most likely mechanism for increasing the quantity of dispersed seeds in a plant–seed disperser assemblage (García and Martínez 2012). Complementarity (also niche or resource partitioning, Hooper et al. 2005) describes the mechanism that additional species are complementary in the use of resources in space and time (Fig. 1B), resulting in an increased aggregate function from the species assemblage. This mechanism explains enhanced pollination functions provided by pollinators that differ in plant choice or timing of foraging activity (Hoehn et al. 2008, Fründ et al. 2013). Similarly, seed dispersers differing in diet, movement and phenology generate a rich and spatially heterogeneous seed rain (Jordano et al. 2007, Bueno et al. 2013, Morales et al. 2013). Finally, interspecific interactions may enhance the aggregate function of an assemblage (Fig. 1C, functional facilitation sensu Klein et al. 2008). Interspecific competition for floral resources may lead to increased fidelity of pollinators for specific floral resources, resulting in increased seed set and aggregate seed production (Brosi and Briggs 2013). Similarly, when honey bees are present, wild solitary bees move frequently between coffee plants in Indonesia and are more efficient pollinators (Klein et al. 2008). Interspecific facilitation may enhance seed-dispersal functions. Since many frugivorous bird species track each other during foraging, large and diverse foraging groups may be most efficient in locating fruit resources and dispersing seeds (Saracco et al. 2004, García and Martínez 2012).

Shapes of BEF relationships

The shape of BEF relationships illustrates the relative contribution of species to the aggregate function (Hooper et al. 2005) as well as the impact of biodiversity change on ecosystem functions in the real world. Different from experiments, in which species are usually added to monocultures, most richness gradients in natural ecosystems actually derive from inverse sequences of species' extinction (Larsen et al.
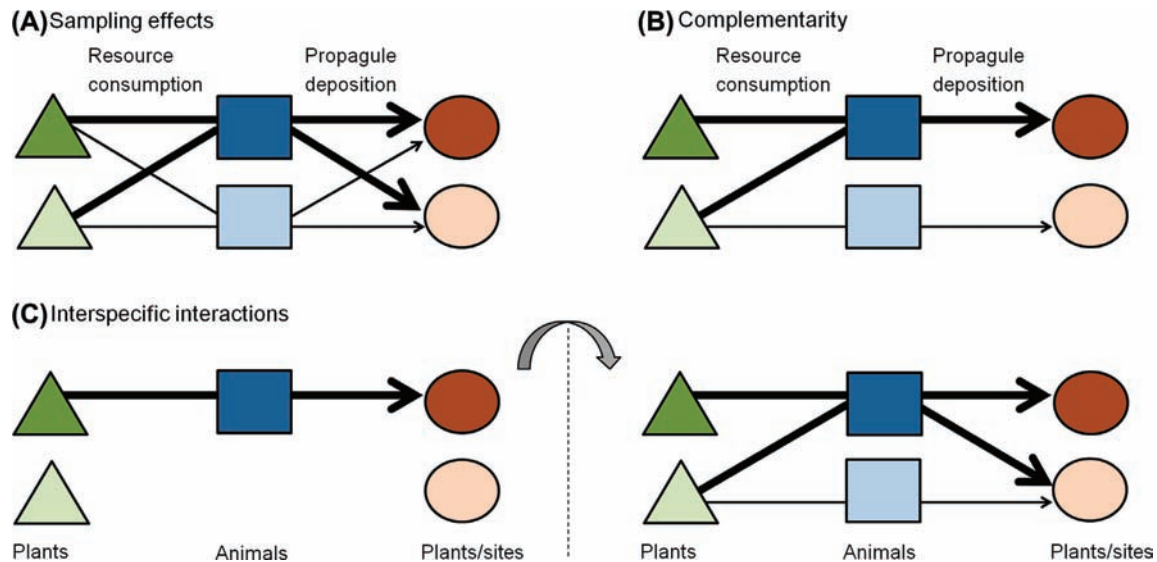
Figure 1. Mechanisms of biodiversity effects on animal-mediated ecosystem functions, such as pollination and seed dispersal. (A) Sampling effects of dominant key species, (B) complementary effects of different species and (C) effects mediated by interspecific interactions, e.g. due to changed foraging behaviour in multispecies animal assemblages. The respective ecosystem function can be influenced by quantitative effects (e.g. the number of pollen or seeds removed and deposited, indicated by arrow width in examples (A–C)) and qualitative effects (e.g. the deposition site of pollen or seeds relative to the consumption site, examples (B–C)). Green triangles indicate plants (different shading for different species), blue rectangles animals, and brown circles plants (for pollinators) or sites (for seed dispersers).

2005). Early BEF studies have distinguished two types of BEF relationships: 1) a linear trend, indicating that species are functionally singular and their effects on the aggregate function are additive (Fig. 2A), or 2) a saturating trend, suggesting that species are functionally redundant and the incorporation of additional species only slightly increases the aggregate function (Fig. 2B, Hooper et al. 2005). The focus on these two types of relationships emerged from experimental studies in which species pools were assembled randomly (i.e. the order of species' addition or extinction was random). In natural ecosystems, however, species differ in their functional importance and in their extinction proneness.
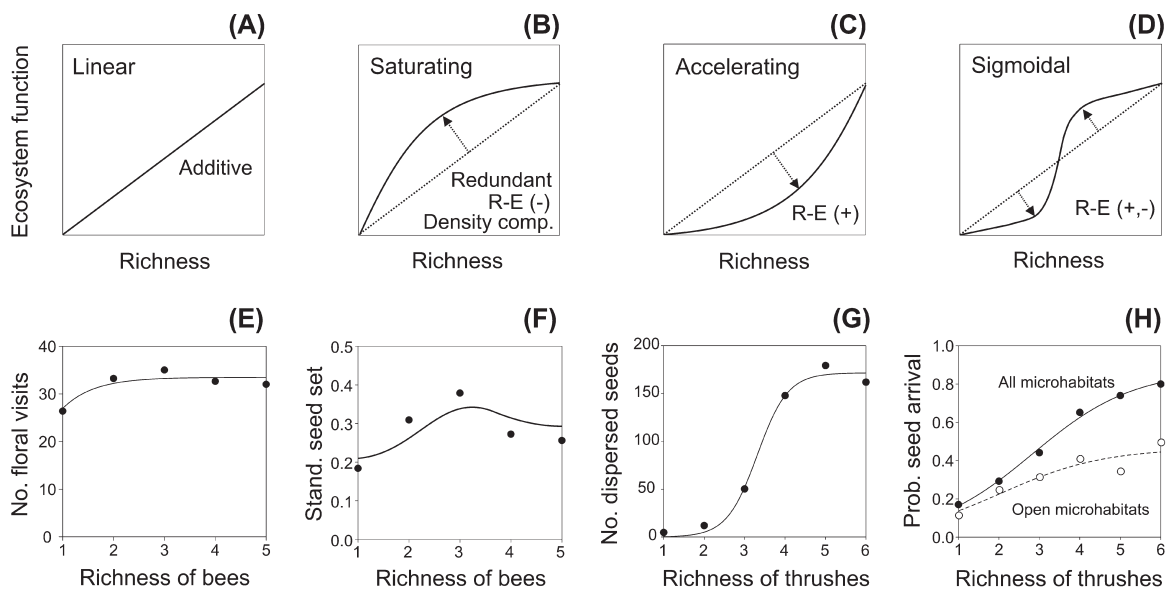

Figure 2. Biodiversity and ecosystem function (BEF) relationships expected for different real-world scenarios: (A) a linear trend (additive roles of species), (B) a saturating trend (redundant roles of species, density compensation and negative response-effect correlation), (C) an accelerating trend (positive response-effect correlation), and (D) a sigmoidal trend (non-linear response-effect correlation). Examples of BEF relationships found for pollination ((E–F); Fründ et al. 2013) and seed-dispersal functions ((G–H); García and Martínez 2012). Pollination quantity is described by the number of bee visits to flowers (E) and quality by the aggregate seed set standardized across plant species (F). Seed-dispersal quantity is given by the number of dispersed seeds per surface unit (G) and quality by the probability of seed arrival across the whole landscape or to open microhabitats (H). Smoothing curves were fitted to illustrate different shapes of BEF relationships (E–H).

While the functional importance depends on the abundance and the phenotypic effect traits of species, their extinction proneness depends on their rarity and their susceptibility to perturbation mediated by their response traits (Hooper et al. 2005, Suding et al. 2008, Luck et al. 2012). Thus, BEF relationships in natural ecosystems differ depending on the relationship between functional importance and extinction proneness across species (i.e. the correlation between response and effect traits, Larsen et al. 2005). An accelerating trend is expected when the least susceptible species are functionally less important than extinction-prone species (positive response-effect correlation, Fig. 2C). By contrast, a saturating trend is expected when the least susceptible species are functionally most important (negative response-effect correlation, Fig. 2B). Depending on the correlation between functional importance and extinction proneness, other shapes of BEF relationships can emerge, for instance a sigmoidal trend (species with intermediate extinction proneness are functionally most important, Fig. 2D). Changes of species richness in natural ecosystems could imply changes in the total abundance of the assemblage, although density compensation by the remaining species may occur in response to species loss (Larsen et al. 2005). Density compensation leads to saturating trends in BEF relationships if numerical responses of remaining species compensate for the loss of function (Fig. 2B, Larsen et al. 2005). Thus, the presence of density compensation could reshape BEF relationships, but its importance in real-world settings is uncertain (Winfree 2013). Density compensation is more likely to be important in experimental settings that either control total resources (additive experiments) or enforce it directly by controlling abundances (substitutive experiments).

Different BEF relationships have been found in pollination and seed-dispersal studies, depending on the underlying mechanisms, the type of functional component (e.g. quantitative vs qualitative component), the spatiotemporal scale of observation (García and Martínez 2012, Winfree 2013), as well as the studied ecosystem (e.g. mainland vs island ecosystems, Schleuning et al. 2014a). An accelerating trend of functional performance was found along a gradient of increasing bee richness, resulting from a positive correlation between response and effect traits (i.e. body size, Larsen et al. 2005). In an experiment with controlled abundance (Fründ et al. 2013), pollination quantity barely increased with bee richness, suggesting species' redundancy (Fig. 2E). Pollination quality, however, showed an increasing trend indicating complementarity, although it saturated at intermediate richness values suggesting that complementarity depends on which bee species are combined (Fig. 2F). In a seed-dispersal system (García and Martínez 2012), quantitative components showed a sigmoidal relationship with avian disperser richness along a gradient of forest loss (Fig. 2G), suggesting intricate relationships between species' susceptibility to forest loss and their quantitative importance, as well as redundancy among species at high disperser richness. Seed-dispersal quality increased linearly with disperser richness, suggesting additive effects of birds with complementary roles, especially in terms of their spatial movements (Fig. 2H). These examples suggest that complementarity of species may be responsible for stronger diversity effects on qualitative than on quantitative components of ecosystem

functions. Function quality appeared to increase when bee visits were distributed more evenly among plants (Fründ et al. 2013) and when birds differed in habitat use (García and Martínez 2012).

Stability of ecosystem functions

Biodiversity matters for the magnitude of aggregate ecosystem functions, but also for its stability in space and time (Hooper et al. 2005). Diverse pollinator and seed-disperser assemblages provide more stable and persisting functions than depauperate assemblages (Fontaine et al. 2006, García et al. 2013). The increased stability in diverse assemblages (known as the insurance hypothesis, Yachi and Loreau 1999) may emerge from different, albeit conceptually related mechanisms. Asynchronous spatiotemporal fluctuations in population dynamics of functionally similar species can stabilize ecosystem functions across space and time (portfolio effects, Loreau 2010). This is similar to density compensation by functionally redundant species after species loss (Winfree and Kremen 2009). Insurance effects may also result from different species' responses to disturbance. If responses of functionally similar species differ, some species will be able to resist perturbation and the aggregate function will be maintained (response diversity, Suding et al. 2008, Winfree and Kremen 2009). Different susceptibilities of species to perturbation may operate at different spatiotemporal scales and lead to cross-scale resilience of ecosystem functions (Winfree and Kremen 2009).

Functional diversity and ecosystem functions

The variability in BEF relationships as well as the concept of response diversity suggests that the number of species (i.e. taxonomic richness) does not necessarily match the number of different functional roles in a species pool (i.e. functional diversity, Díaz et al. 2007, 2013) because species may be functionally additive or redundant (Winfree 2013) and may differ in their extinction proneness under certain scenarios (Suding et al. 2008). Simple measures of functional diversity, such as the number of functional groups, defined by foraging traits (e.g. tongue length) or behaviour (social vs solitary bees), have been shown to be better predictors of pollination functions than taxonomic richness (Hoehn et al. 2008, Albrecht et al. 2012). Furthermore, sophisticated measures have been proposed to quantify the functional variability among species, by projecting species into a multidimensional trait space (Villéger et al. 2008), according to the traits that influence the respective function (functional traits, Violle et al. 2007). Such projections allow to quantify the number of functional roles, that is for instance reflected by the volume of the functional space (i.e. functional richness), or the distribution of functional roles, such as the regularity of distances between species (i.e. functional evenness). Such approaches are also promising to quantify the variability in functional roles within assemblages of animal pollinators or seed dispersers (Plein et al. 2013, Dehling et al. 2014a). Thus far, however, no study has explicitly tested how these functional metrics translate into different components of pollination and seed-dispersal functions.

Plant–animal mutualistic networks

Mostly independent of BEF research, the structural diversity of the interactions between plants and their pollinators and seed dispersers has been studied by ecological network analysis. The traditional approach to study these mutualisms mostly focused on one or two plant species, but plants usually share mutualists with multiple plants in the community (Waser et al. 1996). Plant–animal mutualistic associations started to be described as networks of nodes (species) interconnected by links (interactions) after the seminal paper by Jordano (1987). In difference to food webs, mutualistic networks are bipartite, meaning that interactions between two sets of species (plants and animals) are considered. Links between species can be described as present/absent (binary or qualitative networks) or an estimate of interaction strength, typically interaction frequency (e.g. number of visits by pollinators or seed dispersers or number of pollen or seeds removed), can be assigned (quantitative or weighted networks). While theoretical treatment is more established for binary networks, quantitative networks have gained importance because sampling effects are usually more problematic for binary than for weighted networks (Banašek-Richter et al. 2004, Blüthgen et al. 2008). Furthermore, functional effects are better inferred from interaction frequency (Vázquez et al. 2005, 2012). Many studies have described network structure by means of aggregate network properties (Ings et al. 2009, Vázquez et al. 2009). There is also a growing body of theory about the potential consequences of network structure for the functioning and the stability of ecological communities (Tylianakis et al. 2010, Blüthgen and Klein 2011). Nevertheless, empirical demonstration of these consequences is mostly missing and thus far most network studies have been focused on describing the structural properties of networks and usually lack the link between network structure and ecosystem functioning.

Structure and determinants of mutualistic networks

Important structural properties of networks are nestedness and modularity (Bascompte and Jordano 2014). Nestedness describes a pattern in which small assemblages are subsets of larger assemblages, i.e. specialists interact with a subset of the species that generalists interact with (Bascompte et al. 2003). This is closely related to the concepts of asymmetric specialization, i.e. that specialists interact with generalists and vice versa (Vázquez and Aizen 2004), and skewed degree distributions, i.e. most species have few links and few species have many links (Jordano et al. 2003). Although empirical networks are not perfectly nested, most empirical mutualistic networks show a more nested structure than expected for random networks (Bascompte et al. 2003). However, the prevalence of nestedness and asymmetric specialization could partly derive from sampling effects as the number of observations is typically unevenly distributed across species (Vázquez and Aizen 2004, Blüthgen et al. 2008). Modularity (or compartmentalization) is a pattern where species fall into groups (modules, compartments or clusters) of species that interact more closely with each other than with species from other modules (Olesen et al. 2007, Schleuning et al.

2014b). Although completely separated compartments are rarely found, studies looking for modularity in mutualistic networks tend to find a modular structure corresponding to biological traits, such as phenology or morphology (Olesen et al. 2007, Mello et al. 2011, Martín González et al. 2012, Schleuning et al. 2014b).

Another important part of network structure is complexity, which can vary independent of nestedness and modularity. Popular measures of complexity are connectance (the proportion of realized links in binary networks, Jordano 1987) and different measures of interaction diversity that can be calculated analogous to community measures of species diversity (Bersier et al. 2002, Tylianakis et al. 2007). Similarly, the evenness of interactions describes to what extent a quantitative network is dominated by a few strong interactions (Tylianakis et al. 2007, Plein et al. 2013). Based on the concept of interaction diversity, Blüthgen et al. (2006) suggested a standardized metric of interaction diversity (H_2') that controls for the influence of community composition and species frequency and is maximized when species differ most in their resource use. It is thus interpreted as a measure of niche partitioning and specialization (Blüthgen 2010) and tends to be slightly higher in pollination than in seed-dispersal networks (Schleuning et al. 2012).

Apart from describing the structure of mutualistic networks, studies have tried to identify the determinants of this structure (Vázquez et al. 2009), i.e. evaluate how species traits predict either aggregate network properties (Santamaría and Rodríguez-Gironés 2007) or pairwise interactions and their strength (Stang et al. 2009, Maglianesi et al. 2014). In a conceptual framework, one can roughly distinguish between abundance-driven and trait-driven effects on network structure (Vázquez et al. 2009, Blüthgen 2010). Species' relative abundances are a major determinant of interaction probabilities and the impact of a species in a network (Blüthgen 2010, Vázquez et al. 2012). Such abundance effects are mediated by species' frequency or activity in the network and are usually independent of niche differentiation among species with respect to their mutualistic partners. In practice, abundance effects on network structure may be difficult to separate from effects related to the number of observations per species, which are also associated to sampling effects, and thus should be interpreted carefully (Blüthgen 2010). Trait effects refer to effects of phenotypic traits that modify the probability of interactions for plant–animal pairs. Typically, multiple traits jointly determine the pattern of who interacts with whom (Junker et al. 2013, Dehling et al. 2014b), consistent with the concept of pollination and seed-dispersal syndromes (Faegri and van der Pijl 1966, van der Pijl 1982). Traits that influence the matching between interaction partners include morphology (e.g. floral size and shape vs body size and shape), appearance (e.g. floral colour vs visual system), chemistry (e.g. floral odor and rewards vs olfactory and metabolic systems; Pyke and Waser 1981, Wheelwright 1985, Stang et al. 2009, Junker et al. 2013), as well as spatiotemporal matching of species' occurrence, for instance due to phenological matching (Martín González et al. 2012, Plein et al. 2013).

Mutualistic networks and ecosystem stability

One important focus of network studies has been the relationship between network structure and ecosystem stability (Bascompte and Jordano 2014). A central stability concept in network ecology is network robustness, i.e. the likelihood of secondary species' extinctions after species loss (Memmott et al. 2004). The robustness of networks to species' extinction is closely related to the redundancy (or complementarity) among species in mutualistic networks. Network robustness against secondary species' extinctions usually increases with the degree of redundancy in a network (Box 1). In a highly nested network, specialist species are supposed to be functionally redundant, whereas core species are functionally important for the whole network (Bascompte and Jordano 2007). In contrast, the concept of modularity stresses the complementarity of species belonging to different modules (Olesen et al. 2007). Species in a modular network may be redundant within a module, but complementary between modules. Similar to the concepts of nestedness and modularity, network complexity is also associated with the degree of complementarity in the network. Networks with a high degree of niche partitioning (specialized networks sensu Blüthgen et al. 2006) are characterized by complementary species, whereas redundancy is high in generalized networks with a high degree of niche overlap (Blüthgen and Klein 2011). Overall, highly connected networks dominated by generalized interactions should be rather robust against extinctions (Dunne et al. 2002, Memmott et al. 2004), and networks dominated by strong interactions may be instable (Rooney and McCann 2012). The relationship between network structure and ecosystem stability depends, however, on the sequence of species' extinction (Kaiser-Bunbury et al. 2010). The robustness of a network is, thus, also associated with the extinction proneness of the species in the network, which is consistent with the predictions of the response-effect framework in BEF research (Larsen et al. 2005).

Integrating mutualistic networks into BEF research

The integration between the fields of BEF and mutualistic network research requires differentiating between three levels of biological organization that are determined by a sequence of different processes. The three levels are the assembly of ecological communities by environmental filtering, the formation of interaction networks from the local communities and the mutualistic interactions providing the ecosystem function (Fig. 3). We propose to integrate these levels in a framework that categorizes species traits by the respective organizational level and introduce the framework with a conceptual top-down model describing the effects of animal mutualists on plants and the respective ecosystem function (Fig. 3). Our framework extends the classical response-effect framework (Naeem and Wright 2003), as well as a recent trait-based bottom-up model of trophic interactions (Lavorel et al. 2013), by explicitly incorporating network structure for predicting the consequences of biodiversity loss for ecosystem functioning.

A trait-based model for BEF relationships in mutualistic networks

Community assembly has been described as a process of environmental filtering (Naeem and Wright 2003, Mayfield et al. 2010). Gradients in biodiversity in natural communities are usually the consequence of filtering processes involving species' extinction (Mayfield et al. 2010). The extinction proneness of species is closely related to species traits that mediate their responses to environmental conditions (response traits, Suding et al. 2008, Luck et al. 2012). In our conceptual example, an important response trait related to the susceptibility of avian seed dispersers to human disturbance is avian body size (Galetti et al. 2013). Therefore, big species would be more likely to disappear from a local community (or to decrease in abundance), whereas small species are likely to increase in relative abundance (Fig. 3A). Hence, the model proposes that trait-based filtering determines the local community and its structural and functional diversity (Mayfield et al. 2010).

Contingent on this filtering process, interaction networks are formed because species can only interact if they co-occur in space and time. For network assembly, we primarily view the mutualistic interactions from a resource-consumer perspective (e.g. pollinators and seed dispersers foraging for plant rewards). Accordingly, the composition of the local plant and animal communities would directly determine network structure, if abundance effects dominated the network. Such a network would be highly nested or highly connected, and saturating BEF relationships would be expected (Fig. 2B), due to a high redundancy among species. However, network structure results from the combined effects of species' abundance and phenotypic matching traits (Fig. 3B). In modular networks with a high degree of trait matching within modules, linear BEF relationships would be expected (Fig. 2A), due to additive effects of species with complementary roles in different modules. In the conceptual example, abundant animal species may be functionally important for many plant species. In addition, the matching of beak and fruit morphology mediates complementary effects of animal mutualists on seed dispersal of specific plant species. Hence, a high diversity of the functional roles of animal mutualists ensures high interaction diversity across the entire plant community. This resonates with the idea to measure the redundancy of animal-mediated mutualistic services to plants by the realized diversity of their mutualistic partners (Albrecht et al. 2013). In addition to effects of complementarity, a high diversity of animal mutualists also increases the redundancy of the community and might also increase its response diversity. In the long term, the stability of the network is thus promoted by the occurrence of various species with similar morphologies, enhancing network robustness. Our conceptual model proposes that high functional and interaction diversity of animal mutualists promotes the provisioning and stability of ecosystem functions.

Evaluating the consequences of mutualistic interactions for ecosystem functions changes the focus from an animal-centered perspective, as in most network studies, to a plant-centered perspective, as in most studies of ecosystem functioning. Specifically, the consequences of particular interactions for seed-dispersal or pollination functions

Box 1. Robustness of mutualistic networks to species' extinction

The robustness of networks to species' extinction is closely related to the redundancy (or complementarity) among species in mutualistic networks. For example, different pollination networks may represent a high degree of niche partitioning (high floral trait diversity and high specialization of pollinators; complementarity network, Fig. B1A) or a high degree of niche overlap (low floral trait diversity and low specialization of pollinators; redundancy network, Fig. B1B). Network robustness is illustrated with an example of sequential pollinator extinction, independent of species' traits, for the two types of networks. Secondary extinctions of plants only occur in the complementarity network (Fig. B1A) whereas all plants receive flower visits even after removing many pollinator species in the redundancy network (Fig. B1B). In addition to niche overlap among pollinators, pollinator diversity also contributes to network robustness; as there are more pollinators than plants, networks are less vulnerable to pollinator than plant extinction.
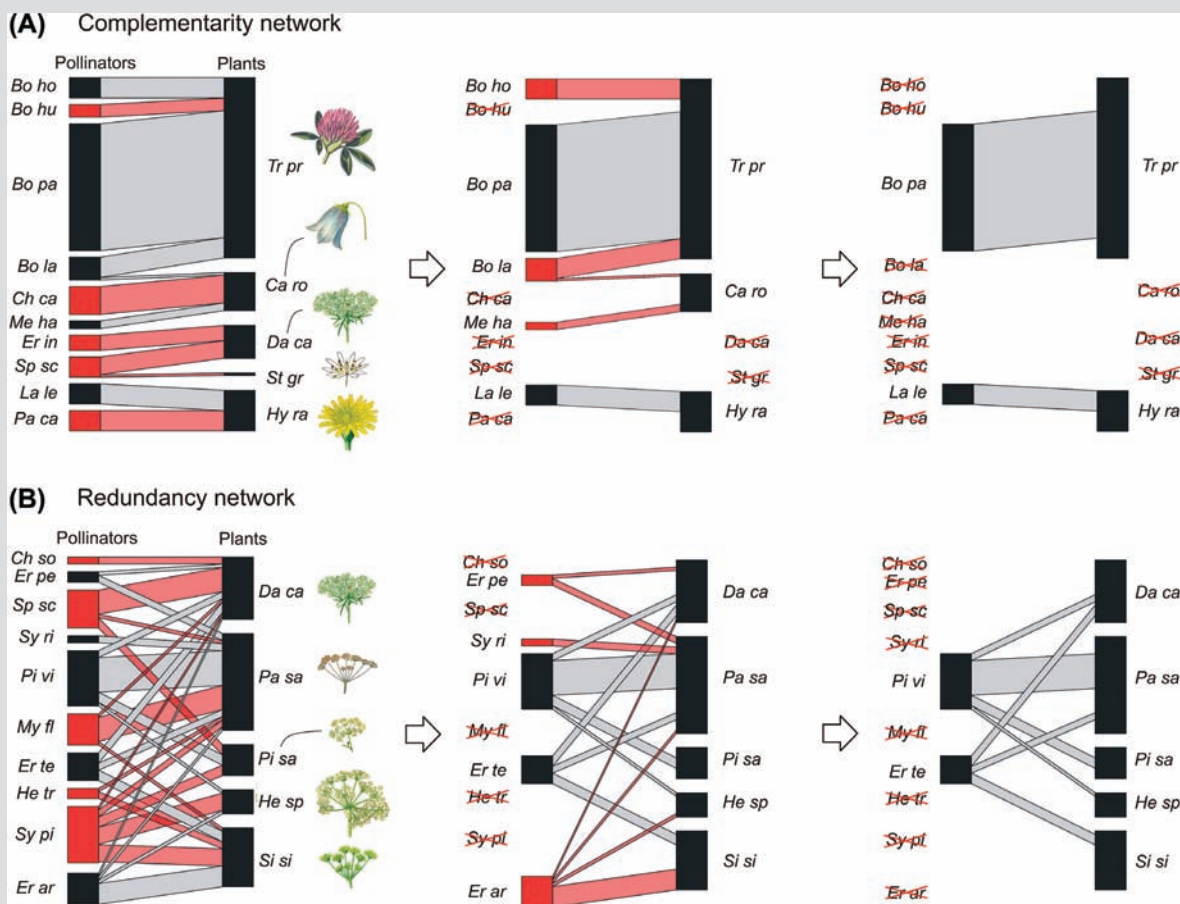

Figure B1. Pollination networks illustrating the concepts of network robustness: (A) high degree of niche partitioning and (B) high degree of niche overlap. We illustrate an example of sequential pollinator extinction in two steps: five pollinator species are lost in a first step (centre column), three pollinator species in a second step (right column). Pollinators prone to extinction in the next step and their links are coloured in red, extinct pollinator and secondarily extinct plant species are crossed out. The complementarity network (A) comprises the ten main pollinators of five plant species differing in floral traits. The redundancy network (B) comprises five flower species with similar floral traits (all Apiaceae) and their hover-fly pollinators. The example networks represent subsets of pollination networks from meadows in Germany (bar width indicates species' interaction frequencies); abbreviations: (pollinators) *Bo ho*: *Bombus hortorum*, *Bo hu*: *Bombus humilis*, *Bo pa*: *Bombus pascuorum*, *Bo la*: *Bombus lapidarius*, *Ch ca*: *Chelostoma campanularum*, *Me ha*: *Melitta haemorrhoidalis*, *Er in*: *Eristalis interrupta*, *Sp sc*: *Sphaeophoria scripta*, *La le*: *Lasioglossum leucozonium*, *Pa ca*: *Panurgus calcaratus*, *Ch so*: *Chrysogaster solstitialis*, *Er pe*: *Eristalis pertinax*, *Sy ri*: *Syrphus ribesii*, *Pi vi*: *Pipizella viduata*, *My fl*: *Myathropa florea*, *Er te*: *Eristalis tenax*, *He tr*: *Helophilus trivittatus*, *Sy pi*: *Syritta pipiens*, *Er ar*: *Eristalis arbustorum*; (plants) *Tr pr*: *Trifolium pratense*, *Ca ro*: *Campanula rotundifolia*, *Da ca*: *Daucus carota*, *St gr*: *Stellaria graminea*, *Hy ra*: *Hypochaeris radicata*, *Pa sa*: *Pastinaca sativa*, *Pi sa*: *Pimpinella saxifraga*, *He sp*: *Heracleum sphondylium*, *Si si*: *Silaum silaus* (see Fründ et al. 2010 for details).
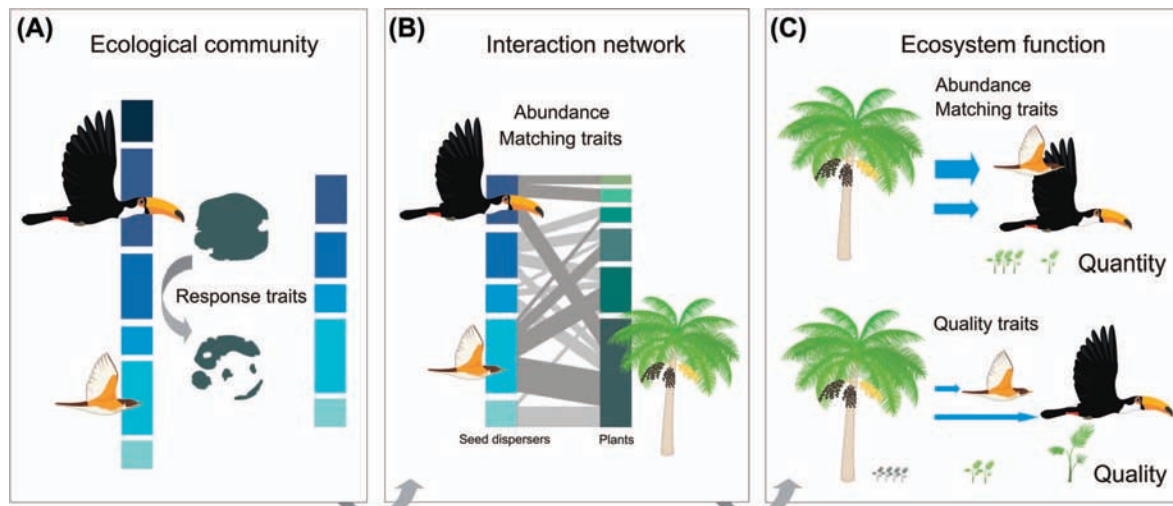
Figure 3. Conceptual framework illustrating the sequential effects of environmental filtering on (A) the composition of the ecological community, (B) network structure and (C) ecosystem functioning. In (A), response traits determine effects of the environmental filter (e.g. habitat fragmentation) on avian species' occurrence and abundance (i.e. consumer diversity); bird species are represented by blue boxes (different shading for different species; body size decreases from top to bottom; box size is proportional to species' abundance), species richness equals the number of boxes. Habitat fragmentation leads to extinction or decreased abundances in large-bodied bird species. In (B), species' abundance and matching traits of seed-disperser and plant species (depicted by green boxes; different shading for different species; smaller fruit size from top to bottom) determine interaction frequencies (i.e. interaction diversity). In (C), abundance and matching traits determine the quantitative seed-dispersal component (e.g. seed removal), and quality traits determine the qualitative component (e.g. seed-dispersal distance). Quantitative and qualitative effects are exemplified for a focal plant species and would be different for another plant species. This conceptual figure illustrates positive relationships between the three types of traits (response: body size; matching: beak size; quality: body size). The framework can be equivalently applied for plant–pollinator networks, e.g. with quantity being the amount of pollen deposited and quality being the proportion of outcross pollen. A similar trait set could be defined for pollinators (response: body size; matching: tongue length; quality: body size).

depend on (quantitative) interaction frequencies and (qualitative) per-interaction effects of an animal mutualist on plant fitness (Schupp et al. 2010). Quantitative components of ecosystem functions are closely associated with interaction frequencies and are thus driven by species abundances and matching traits (Fig. 3C). Qualitative components are related to another set of species traits that describe the quality of service provided by an animal for a plant species, irrespective of interaction frequency (quality traits, Fig. 3C). In the conceptual example, quality traits of seed dispersers would be related to mobility and associated seed-dispersal distances (McConkey and Brockelman 2011). At the community level, a high diversity of quality traits in the disperser community would ensure a spatially heterogeneous seed rain (Jordano et al. 2007), favouring species' coexistence. Similarly, a high diversity of quality traits in a pollinator community might ensure high conspecific pollen deliveries and increase plant reproduction, especially under spatially heterogeneous plant distributions (Tylianakis et al. 2008). Both matching and quality traits are effect traits (sensu Suding et al. 2008, Luck et al. 2012), as the product of quantitative and qualitative effects drives the functional importance of a species in the ecosystem (Schupp et al. 2010).

Trait relationships across different organizational levels

Our conceptual model describes a trait-based framework for the effects of biodiversity on multispecies interactions and

cross-trophic functions. In the previous section, we have proposed to distinguish between response, matching and quality traits that mediate the impacts of an environmental filter from the community over the interaction level to the functional impact on the ecosystem. First, response traits determine the diversity of mutualists after environmental filtering. Second, matching traits determine niche partitioning among species and are conceptually related to coexistence traits that favor niche partitioning and coexistence (Hillebrand and Matthiessen 2009). Third, quality traits mediate the functional effects of the mutualistic interactions to the plant community (Díaz et al. 2013).

The susceptibility of an ecosystem function to biodiversity loss depends on the relationship between the different sets of traits. Ecosystem consequences of biodiversity loss would be most severe (e.g. an accelerating BEF relationship, Fig. 2C) in systems with positive response-matching-quality relationships. This would be expected if the same or collinear species traits would matter at different levels in a similar way (Larsen et al. 2005, Hillebrand and Matthiessen 2009). For example, this would be the case in a scenario in which big dispersers are most susceptible to human impact (Galetti et al. 2013), beak size is a crucial matching trait (Wheelwright 1985), and body size is positively related to seed-dispersal distance (Díaz et al. 2013, Fig. 3). By contrast, the consequences of biodiversity loss for ecosystem functions would be less severe (e.g. a saturating BEF relationship, Fig. 2B) if traits varied independently or negatively at different organizational levels or if matching traits were less important than species' abundance for structuring the network, promoting a compensation for

species loss. For instance, large bees may be less susceptible to habitat fragmentation than small bees and thus could maintain their important functional role as pollinators also in fragmented landscapes (Bommarco et al. 2010).

BEF relationships for quantitative and qualitative components of ecosystem functions

In extension to previous concepts (Reiss et al. 2009, Lavorel et al. 2013), we suggest to distinguish between quantitative and qualitative components of animal-mediated ecosystem functions. Different BEF relationships are expected for quantitative and qualitative components because they emerge from different processes and could be influenced by different traits (Fig. 3C). To apply the quantity-quality framework to biodiversity gradients in natural ecosystems, we need a better mechanistic understanding on how environmental variability and species traits shape the link between network structure and ecosystem functions. Studies on seed dispersal suggest that different BEF relationships may be expected for quantitative and qualitative components, depending on the network structure that emerges from the response of animal mutualists to different environmental scenarios (Box 2).

Most importantly, we need to incorporate quantitative and qualitative components in the estimation of interaction strength in mutualistic networks (Carlo and Yang 2011). We suggest employing the concept of effectiveness that is based on the multiplicative effects of interaction frequencies and per-interaction effects of animal mutualists on plant fitness (Schupp et al. 2010). According to this concept, frequency-based interaction networks (e.g. based on visitation frequency or pollen or seed removal) must be transformed to effect networks (i.e. network that represent the functional effects of animals on plants), by adjusting the unit of interaction strength. This could be achieved by multiplying interaction frequencies with a transition probability from pollen removal to seed set or from seed removal to seedling recruitment (Fig. 4). This transition probability may be approximated by a measure of pollination quality, e.g. the proportion of deposited conspecific pollen (Brosi and Briggs 2013), or seed-dispersal quality, e.g. seed-dispersal distance (Díaz et al. 2013). The quality of pollinators or seed dispersers depends on specific animal traits (quality traits) and it is therefore a reasonable assumption that quality is correlated across plant species for a particular animal mutualist. For instance, seed-disperser species are likely to remove seeds of different plant species similarly and, due to their larger home ranges, big species would usually move seeds over longer distances than small species (Morales et al. 2013). Nevertheless, a matrix of transition probabilities for pairs of interacting species would be most appropriate, taking into account that qualitative effects of animals could vary among plant species or plant functional groups. Depending on the type of relationship between the quantitative and qualitative contributions across animal species, we find distinct effect networks (Fig. 4). A positive correlation between quantitative and qualitative components (frequent species are high-quality pollinators or seed dispersers) decreases interaction evenness (i.e. leads to a highly skewed distribution of functional effects, Fig. 4A), and reinforces functional differences among

species. By contrast, a negative quantity-quality correlation (frequent species are low-quality pollinators or seed dispersers) increases interaction evenness (i.e. a more uniform distribution of functional effects; Fig. 4B) and alters the rank of functional importance across animal species (see also Carlo and Yang 2011). Different scenarios of quantity-quality correlations would also lead to changes in BEF relationships. Assuming a random extinction sequence, a positive correlation would result in a saturating BEF response, due to the functional dominance of a few species, and a high aggregate function (Fig. 4A). A negative correlation would lead to a more linear BEF response, due to functional homogeneity and complementarity among species, and results in a lower aggregate function (e.g. a larger proportion of seeds is deposited beneath parent plants; Fig. 4B). A negative correlation between quantitative and qualitative contributions is a likely scenario for pollination and seed-dispersal functions because species with high interaction frequencies may have small per-capita effects because of their small body size (Larsen et al. 2005, Díaz et al. 2013). However, studies on the relationships between quantitative and qualitative contributions of consumer species in mutualistic networks are rare (Vázquez et al. 2005, 2012), especially at a species by species resolution. Because of these uncertainties, the conceptual example represents two extreme scenarios and demonstrates that the interpretation of network structure in a BEF context is contingent on the relationship between quantitative and qualitative effects of animal mutualists on ecosystem functions.

Future research directions

We propose integrating the concepts of BEF and ecological network research. We foresee that this integration will improve our understanding of how biodiversity relates to ecosystem functioning in multispecies assemblages by unifying structural and functional approaches in biodiversity research (Thompson et al. 2012). Applying the concept will be valuable for assessing functional consequences of species' extinctions for different types of ecosystem functions along human-induced disturbance gradients. Empirical studies employing this concept will contribute to a better understanding of the impacts of human-induced changes on network structure and ecosystem functioning (Tylianakis et al. 2007, Menke et al. 2012, Weiner et al. 2014). Thus far, there is a lack of such empirical studies and theoretical simulations testing the robustness of network structure against perturbation are often grounded on uncertain scenarios. Our synthesis, thus, also calls for more studies of ecological networks and ecosystem functions along human-induced disturbance gradients.

The cornerstone of our concept is a trait-based understanding of the sequential processes that determine BEF relationships in natural ecosystems (Fig. 3) and the application of the concept to a specific ecosystem function and environmental context requires two main steps. First, to test changes in ecosystem functioning in response to species loss, it is necessary to identify relevant species traits mediating responses, matching and functionality of species. Second, it requires defining the quantitative and qualitative components of the

Box 2. Network structure and BEF relationships for quantity and quality of seed dispersal

In the fragmented Cantabrian secondary forests, thrushes are the major seed dispersers of dominant fleshy-fruited trees (García and Martínez 2012, García et al. 2013). Because tree species differ in masting frequency and spatial distribution, the fruiting landscape at a given site changes among years (Fig. B2). In years when fruits are concentrated in large forest patches (masting of holly *Ilex aquifolium*), a dominance of the abundant and forest-related redwing *Turdus iliacus* is expected, leading to a generalized and nested network (Fig. B2A). Consequently, the spatial pattern in seed rain matches the forest distribution and few seeds reach open sites (Fig. B2A). By contrast, in years when fruits are more widespread (masting of hawthorn *Crataegus monogyna*), niche partitioning among thrush species is likely to increase (Fig. B2B). Due to spatial matching between fruiting patterns and thrush habitats, hawthorn fruits are the main diet of thrushes that are prone to visit deforested habitats, such as mistle thrush *T. viscivorus* and fieldfare *T. pilaris* (Fig. B2B). Seed rain in these years is widespread and many seeds reach open sites. The two scenarios lead to distinct BEF relationships along the gradient of forest loss. In the first scenario, a sigmoidal relationship between seed-dispersal quantity and thrush richness would emerge (Fig. B2A). Weak effects of thrush richness on seed-dispersal quality would be expected. In the second scenario, a strong positive relationship between seed-dispersal quality and thrush richness would be expected from complementary effects of thrush species (Fig. B2B).
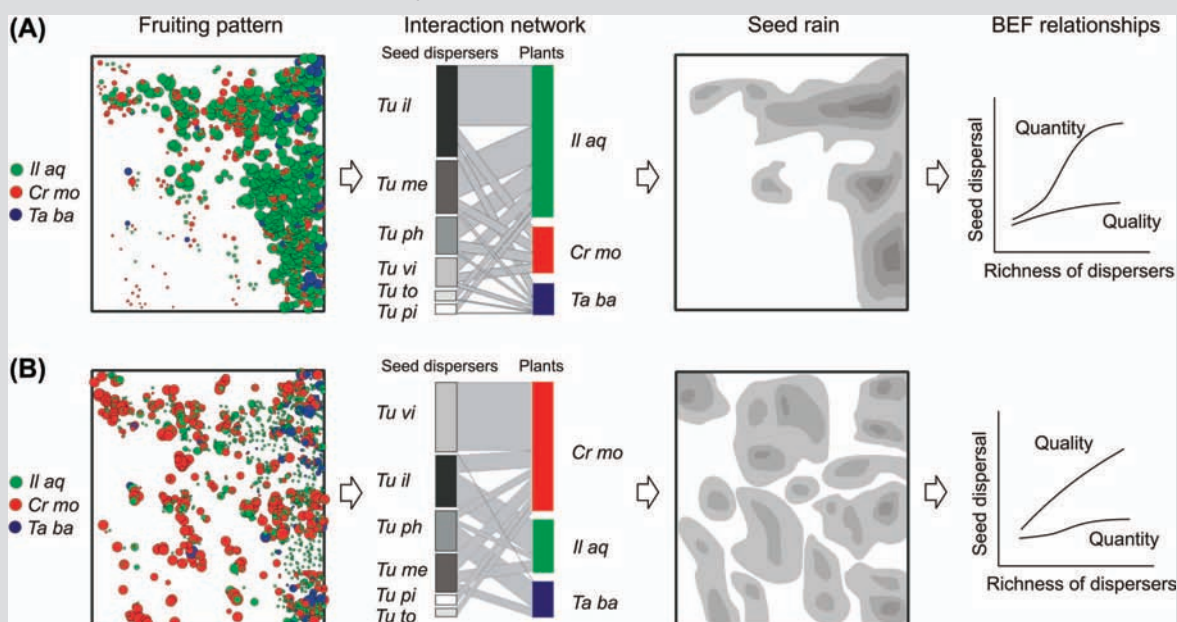

Figure B2. Fruiting landscapes, interaction networks, seed rain and BEF relationships for the Cantabrian secondary forests. The left panels represent two fruiting scenarios in different years in the same plot (400 × 440 m), with dots representing trees within a non-forest (white) matrix, colours species, and dot size being proportional to fruit crop. The seed rain represents the distribution of dispersed seeds of all tree species (different grey shading for different seed density). Seed dispersal quantity represents the number of seeds per surface unit, whereas quality the probability of dispersal to non-forest matrix. Abbreviations: *Il aq*: holly; *Cr mo*: hawthorn; *Ta ba*: yew; *Tu il*: redwing; *Tu me*: blackbird; *Tu ph*: song thrush; *Tu vi*: mistle thrush; *Tu pi*: fieldfare; *Tu to*: ring ouzel.

particular ecosystem function. This is conceptualized in the identification of an adequate effect network that integrates information on pair-wise interaction frequencies and the functional outcome of the respective interaction. Based on a matrix of potentially important traits and the representation of the effect network, it will be possible to formulate specific hypotheses about the shape of the BEF relationship and the stability of an ecosystem function after species loss. Although we are aware that we lack comprehensive datasets of mutualistic networks and species traits for many systems, employing the conceptual model will also be valuable for directing targeted field studies and trait surveys. For instance, animal mutualists could be classified into functional groups of species according to their effects on a specific ecosystem function (e.g. according to their potential distances of pollen or seed dispersal). Such trait-based classifications reflecting different functional roles of species would be a first step towards the implementation of BEF concepts into mutualistic network research.

We have exemplified how the proposed concept could be implemented for improving our understanding of BEF relationships for seed-dispersal and pollination functions. The concept can also be applied to investigate changes in other types of ecological networks and ecosystem functions
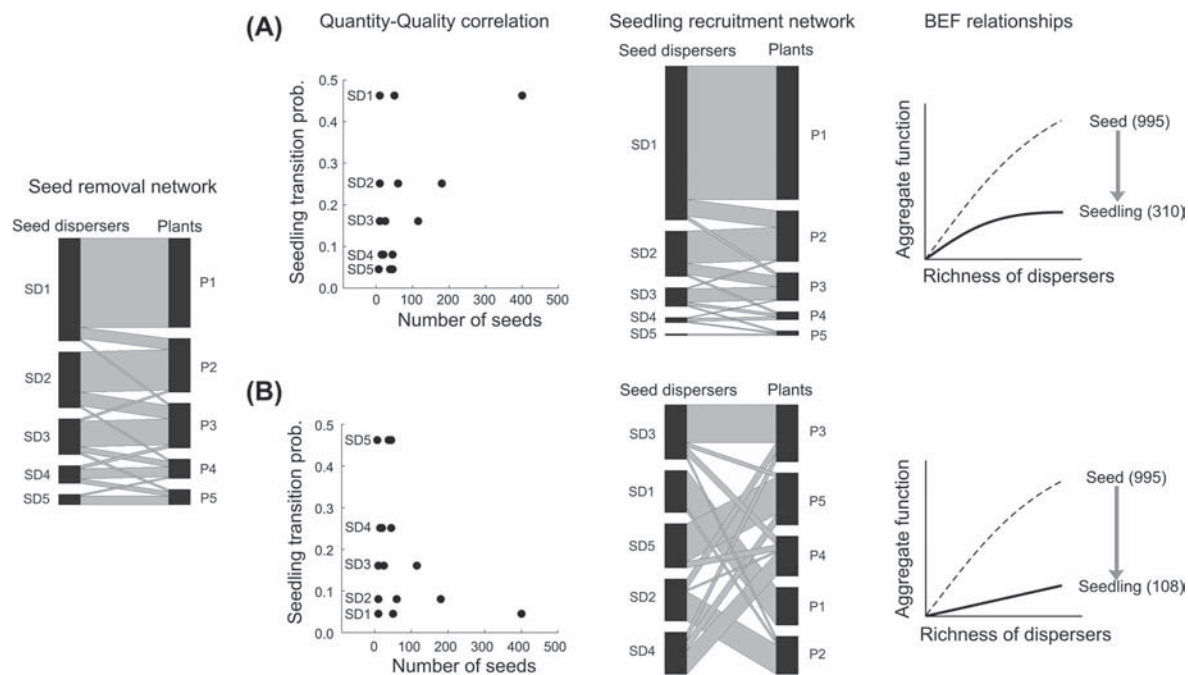
Figure 4. Conceptual example showing how to transform a seed-dispersal network into an effect network by employing the concept of seed-dispersal effectiveness; abbreviations SD1–SD5 and P1–P5 indicate different species of seed dispersers and plants, respectively. The transformation involves the multiplication of seed-removal frequencies (quantitative component; the total number of removed seeds is 995) with a transition probability describing the transition from seed removal to seedling recruitment (qualitative component). The transition probability is approximated by an animal-specific measure of seed-dispersal quality across all plant species (i.e. by a vector of transition probabilities describing the effect of each animal species on all plant species). Different correlations of quantitative and qualitative contributions of consumer species result in distinct effect networks and changes in BEF relationships (assuming a random sequence of seed-disperser extinction): (A) a positive correlation decreases evenness and would lead to a saturating BEF shape; (B) a negative correlation increases evenness and would lead to a linear BEF shape. In (A), the aggregate function of the entire seed-disperser assemblage (i.e. the number of established seedlings, estimated from applying the matrix of transition probabilities to the number of seeds dispersed by each animal species) is higher than in (B). Equivalently, the quantity-quality correlation could be defined for plant–pollinator interactions, e.g. by the number of pollinator visits and the contribution to seed set per visit or by the number and origin of pollen grains deposited.

along environmental gradients. The concept is applicable to all types of bipartite species interactions in which matching traits can be identified, which is true for most resource–consumer relationships, including antagonistic interactions such as plant–herbivore or host–parasitoid interactions. Another crucial property of our conceptual model is the distinction between the quantitative and qualitative effects of consumer species, which would also be important for evaluating species-specific or guild-specific effects of herbivores on plants (Crawley 1989). In addition to the extension to other types of interactions, the concept could also be adapted to account for the spatiotemporal variability in interactions (Fründ et al. 2010, Plein et al. 2013, Kissling and Schleuning 2015) and spatiotemporally dynamic interaction niches of species (Fründ et al. 2013). Currently, the conceptual model assumes that the effects of response, matching and quality traits are conserved in space and time and thus neglects context-dependent trait effects.

It is a big challenge for ecology to assess the consequences of global change and biodiversity loss for ecosystem functioning. If we are to understand these consequences, we need to extend our understanding of biodiversity and ecosystem functioning to multispecies interactions and must develop structural network theory into a functional ecosystem theory. We hope that our concept will foster this conceptual integration of BEF and mutualistic network research.

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