

ECOGRAPHY

Review

Functional trait dimensions of trophic metacommunities

Barbara Bauer, Michael Kleyer, Dirk C. Albach, Bernd Blasius, Ulrich Brose, Thalita Ferreira-Arruda, Ulrike Feudel, Gabriele Gerlach, Christian Hof, Holger Kreft, Lucie Kuczynski, Kertu Löhmus, Stefanie Moorthi, Christoph Scherber, Stefan Scheu, Gerhard Zotz and Helmut Hillebrand

B. Bauer (<https://orcid.org/0000-0003-2688-2788>), Inst. for Botany and Zoological Inst. and Museum, Univ. of Greifswald, Greifswald, Germany – M. Kleyer (<https://orcid.org/0000-0002-0824-2974>) ✉ (michael.kleyer@uni-oldenburg.de), D. C. Albach (<https://orcid.org/0000-0001-9056-7382>), G. Gerlach (<https://orcid.org/000000015246944X>), K. Löhmus (<https://orcid.org/0000-0003-0470-6521>) and G. Zotz (<https://orcid.org/0000-0002-6823-2268>), Inst. of Biology and Environmental Sciences, Univ. of Oldenburg, Oldenburg, Germany. – B. Blasius (<https://orcid.org/0000-0002-6558-1462>), U. Feudel, L. Kuczynski (<https://orcid.org/0000-0002-4448-2836>), S. Moorthi (<https://orcid.org/0000-0001-8092-8869>) and H. Hillebrand (<http://orcid.org/0000-0001-7449-1613>); Inst. for Chemistry and Biology of the Marine Environment (ICBM), Univ. of Oldenburg, Oldenburg, Germany. HH also at: Helmholtz Inst. for Functional Marine Biodiversity (HIFMB), Univ. of Oldenburg, Oldenburg, Germany. HH also at: Alfred-Wegener Inst., Helmholtz Center for Polar and Marine Research, Bremerhaven, Germany. – U. Brose, Inst. of Biodiversity, Friedrich Schiller Univ. Jena, Jena, Germany, and EcoNetLab, German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany. – T. Ferreira-Arruda (<https://orcid.org/0000-0003-1385-0226>) and H. Kreft (<https://orcid.org/0000-0003-4471-8236>), Biodiversity, Macroecology and Biogeography, Univ. of Göttingen, Göttingen, Germany. – S. Scheu (<https://orcid.org/0000-0003-4350-9520>), J.F. Blumenbach Inst. of Zoology and Anthropology, Univ. of Göttingen, Göttingen, Germany, and Centre of Biodiversity and Sustainable Land Use, Univ. of Göttingen, Göttingen, Germany. – C. Hof, Terrestrial Ecology Research Group, Technical Univ. of Munich, Freising, Germany. – C. Scherber (<https://orcid.org/0000-0001-7924-8911>), Centre for Biodiversity Monitoring, Zoological Research Museum Alexander Koenig, Bonn, Germany.

Ecography

43: 1486–1500, 2021

doi: 10.1111/ecog.05869

Subject Editor: Dominique Gravel

Editor-in-Chief: Miguel Araújo

Accepted 15 June 2021



www.ecography.org

Metacommunity ecology currently lacks a consistent functional trait perspective across trophic levels. To foster new cross-taxa experiments and field studies, we present hypotheses on how three trait dimensions change along gradients of density of individuals, resource supply and habitat isolation. The movement dimension refers to the ability to move and navigate in space, the tolerance dimension addresses the ability to tolerate prevailing environmental conditions and the interaction dimension aggregates the abilities to acquire resources in competition with other species, to defend against consumers or to profit from other species by mutualism and facilitation. In multi-trophic studies, functionally analogous traits associated to these dimensions need to be defined across taxa and measured. The dimensions represent subnetworks of strongly correlated traits within the overall phenotypic trait network. These subnetworks can be aggregated to trait modules using dimension reduction techniques. We demonstrate how to derive dimensions from species distributions and trait correlation networks, using salt marshes as an example. We hypothesize that at the single-community scale, investments by organisms in the tolerance dimension increase with decreasing resource supply. Investments to the interaction dimension increase with increasing density. Communities with densely packed individuals are characterized by convergence under equal competition and by increasing divergence under stabilizing and equalizing competition. At the metacommunity scale, trade-offs between the movement dimension and the interaction dimension shape the community functional composition. Biomass removal by consumers act as an equalizing factor and increase divergence in the interaction and movement dimension, particularly in well-connected habitats. As future research directions to advance functional metacommunity ecology, we propose investigating 1) the feasibility of using dimensions as broad generalizations

© 2021 The Authors. Ecography published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos
This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

of multiple functions in different meta-ecosystems, 2) functional trait analogues across taxa, 3) dimension responses and effects on gradients of meta-ecosystems and 4) matching of functionally analogous traits between trophic levels.

Keywords: allometry, competition, dispersal, environmental stress, food web, interaction, movement, tolerance, trade-off, trait convergence, trait divergence, salt marsh

Introduction

Over 30 years ago, Schoener (1986) described a ‘mechanistic ecologist’s utopia’ where ‘variation in population and community patterns can be understood as variation in individual-ecological conditions’ (Kearney et al. 2010). Since then, ecologists have made substantial progress on this mechanistic agenda. One crucial step in this process was the gradual consolidation of the concept of functional traits (McGill et al. 2006, Violle et al. 2007), another was the consolidation of isolated concepts regarding species’ responses to ‘filters’ comprising abiotic conditions, biotic interactions and habitat isolation in determining the assembly and functioning of communities (Fig. 1, Keddy 1992, Schleuning et al. 2015, 2020, Brose and Hillebrand 2016, Staniczenko et al. 2017). Functional traits and filters are supposed to be linked by a keyhole principle, i.e. to pass a given filter, organisms need matching trait expressions (Diaz et al. 1998, Weiher et al. 2011). In fragmented landscapes, species need highly developed movement capabilities to pass the isolation filter, in landscapes characterised by environmental stress, such as e.g. salt marshes, species need tolerance mechanisms to prevail, and in resource-rich landscapes, species able to convert resources into competitive advantage will be most abundant (Fig. 1; Grime 2002). While many of the earlier studies dealt with plants, more recent work expanded the relationship between traits and filters to animals. Brousseau et al. (2018) reviewing links between traits of terrestrial arthropods and functions suggested that the most commonly studied functions contribute to four types of processes that affect organismal performance and, consequently, community assembly and dynamics: dispersal, biotic and abiotic filtering, and organismal feedback to the biotic filter. This framework is certainly relevant for other taxa as well, including plants and fungi. However, we argue that organismal feedback should not be restricted to biotic interactions, but also to abiotic filters, due to processes such as niche construction and ecosystem engineering (Fig. 1; Jones et al. 1994).

Simultaneously with the rise of trait-based ecology, the concept metacommunity fostered a mechanistic approach to understand the dynamics of spatially structured communities (Mouquet and Loreau 2003, Leibold et al. 2004, Wang and Loreau 2016). It connects the assembly of single communities to local interactions among species and the dispersal of individuals between communities in space and time (Pillai et al. 2011, Shoemaker and Melbourne 2016). Recent advances have linked trophic networks (Gravel et al. 2011) as well as coexistence and niche theory to metacommunity theory (Letten et al. 2017, Thompson et al. 2020).

Several attempts have already been made to explain metacommunity assembly and dynamics from species traits (Kneitel and Chase 2004, Burns and Neufeld 2009, Schleicher et al. 2011). A recent database lists 80 datasets that can potentially be used to link traits, environment, spatial position and community composition (Jeliakov et al. 2020). Guzman et al. (2019) suggested that further advancement of trophic metacommunity theory needs to consider ‘spatial use properties’ of each trophic level, defined as traits that constrain the spatial and temporal scales of species interactions. The extent of covariation

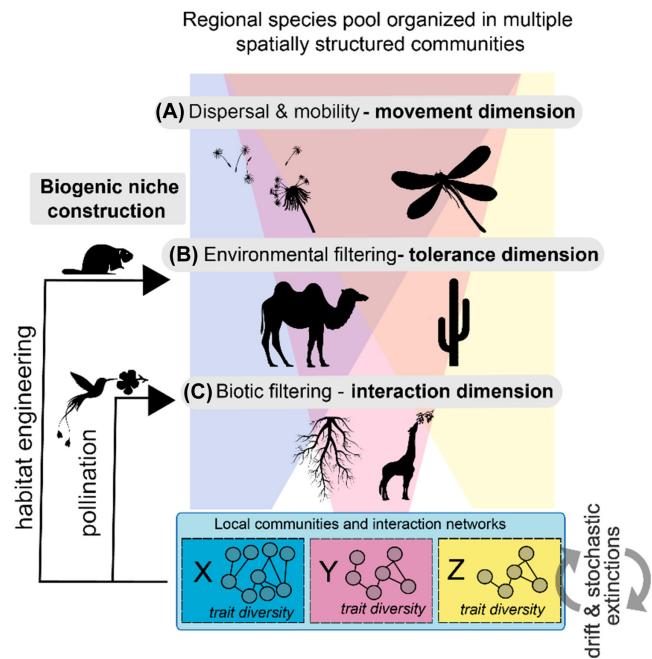


Figure 1. Conceptual diagram illustrating the role of trait dimensions in spatial community ecology. A common view of local community assembly (Weiher and Keddy 1995) is that species immigrate into local communities X, Y, Z from the regional species pool (determined by traits associated with movement (A)) and persist if they are able to tolerate local environmental conditions (determined by traits associated with the tolerance dimension (B)), while competition and trophic interactions allow their coexistence with co-occurring species (determined by traits associated with the interaction dimension (C)). Spatial dynamics and local interactions create individual communities with high or low and convergent or divergent investments of biomass and energy to the traits associated with each dimension. Biogenic niche construction facilitates survival in otherwise unsuitable habitats. Community X is more determined by (A), Y by (B) and Z by (C), although all three dimensions are relevant. Note that in real communities the three filters often act simultaneously.

of these spatial use properties across trophic levels should have strong effects on trophic metacommunity dynamics. Despite these advances, however, we still lack an understanding of how species interactions within and across trophic levels relate to the trait distributions of spatially structured communities. Empirical metacommunity studies explicitly assessing trophic interactions or entire interaction webs are still exceptional, especially at large spatial scales (but see Schleuning et al. 2014).

To unify spatial and trophic aspects of functional ecology (Gravel et al. 2016) and to guide future experiments, we present a framework to derive expected trait distributions in metacommunities along environmental and spatial gradients. Ideally, such a framework is general enough to be applicable to different taxa and concise enough to allow deriving testable hypotheses. Therefore, we suggest three functional trait dimensions that should be central to most organisms, despite strong differences in morphology and physiology between taxa and scales. These dimensions include traits associated with 1) the ability to move and navigate in space ('movement dimension'), 2) the ability to tolerate the prevailing environmental conditions such as high salinity, low temperature or low pH ('tolerance dimension') and 3) the ability to acquire resources in competition with other species, to defend against consumers or to profit from other species by mutualism and facilitation ('interaction dimension') (Fig. 1). In most cases, very different traits are associated with these dimensions among autotrophs and heterotrophs. In this context, Weiss and Ray (2019) introduced the concept of functionally analogous traits, which relate to the same dimension or function in different taxa, even though describing different physiological or behavioral features. In their example, seed size of a plant and hand-wing index of a bird are functional analogues related to the movement dimension. Functionally analogous traits need not be exclusively associated with any of the three dimensions. For instance, locomotory organ traits of animals reflect not only dispersal distance and speed, a component of the movement dimension, but also the maximum speed realized during attacks and escapes as a component of the interaction dimension (Kjørboe 2011). The correlation between the movement dimension and the interaction dimension among aquatic organisms has gained specific attention for its implications on metacommunity processes (Heino et al. 2015) and trait distributions on reefs (Jacquet et al. 2017). Often, low and high values of a specific trait are associated with different dimensions (Spasojevic and Suding 2011). In plants, for instance, small size can be a response to stress in the tolerance dimension (e.g. stress induced by temperature, pH or salinity), and large size a component of the interaction dimension, by shading smaller plants.

Allocation theory and life history theory posit that investments into one trait economically affect investments into other traits to balance fitness benefits against costs leading to tradeoffs or allometries between traits associated

with each of the dimensions (Stearns 1989, Weiner 2004). Investment denotes the amount of matter, energy or information processing allocated to one dimension compared to other dimensions. For instance, 'investment' can be biomass allocation to organs associated with certain dimensions, such as 'reproductive investment' describing the mass ratio between seeds and vegetative tissue in plants (Obeso 2002). Seeds can be associated with the movement dimension, aside from generating offspring, whereas vegetative tissue can be associated with the interaction or tolerance dimension.

Tradeoffs or allometric relationships between traits can be represented by negative or positive correlations. Aggregated over all traits, these correlations form a trait network (Messier et al. 2017). Within such integrated phenotypic networks, subnetworks of strongly correlated traits (Kleyer et al. 2019) can functionally represent the tolerance, interaction and movement dimension (Box 1). The community weighted mean (CWM), i.e. the average dimension value of all species of a community weighted by their abundance, can be used to show how these dimensions change along environmental gradients (Garnier et al. 2007). In multitrophic systems, this approach requires that functionally analogous traits for autotrophs and heterotrophs are identified and associated with the dimensions. Besides the CWM, the variance of functionally analogous trait values around the mean is of great interest to understand community assembly in time and space (Grime 2006). Convergence of trait values reduces the number of functional niches in a community, whereas divergence increases it. Multimodal trait distributions can even render a community trait average meaningless. In a forest exclusively composed of trees and understorey herbs, for instance, the mean plant height may be equivalent to shrubs which are not even present in the community.

In communities structured by trophic interactions, consumer species can reduce or enlarge trait dispersion of the species they prey on and vice versa (Albrecht et al. 2018), provided that consumption is frequency dependent (Pacala and Crawley 1992). Although trophic interactions substantially affect trait means and dispersion of communities, these effects have remained largely unexplored.

In the following, we aim at merging competitive and trophic metacommunity theory with the functional trait concept, using the three general functional dimensions (tolerance, interaction, movement) to facilitate overcoming taxonomical and habitat divides. We begin with a description of the tolerance and interaction dimensions, followed by hypotheses regarding their means and variances, based on a worked example from salt marshes (Box 1). We then extend the framework to spatially structured communities on a habitat isolation gradient and include the movement dimension. Our hypotheses are meant as a starting point for further refinements depending on the specific ecosystem functions and processes considered in a particular study.

Box 1 From species distributions to dimension means and dispersions: an example from salt marshes

An example from saltmarsh plant communities shows a methodological pathway to predictions of dimensions' mean and variances along environmental gradients (Fig. B1, details in the Supporting information). The approach starts with species distribution curves along environmental gradients. In Fig. B1a, this is a gradient of groundwater depth and

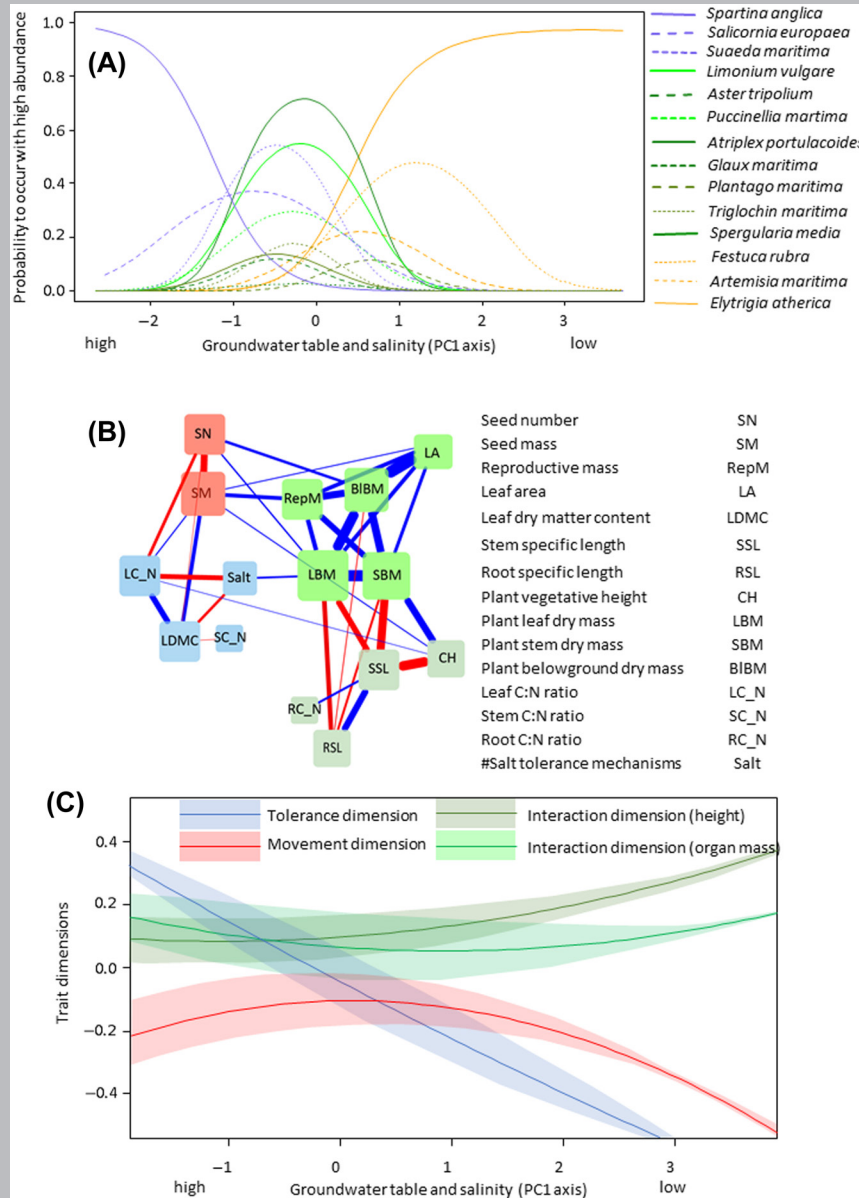


Figure B1. From species distributions to trait subnetworks and community dimension means and variances on environmental gradients: a salt marsh example. (A) Saltmarsh species response curves on a gradient of correlated environmental conditions (PC1 axis of groundwater table and salinity). Data sampled on 62 plots located on Mellum and Spiekeroog islands, Lower Saxony, Germany. Blue lines: pioneer species, green lines: lower saltmarsh species, orange lines: upper salt marsh species. (B) Identification of dimensions of strongly correlated traits in a trait correlation network. Trait box size denote the number of connections to this trait, color the membership to a trait module. Connection size shows correlation strength, the smallest size with $r > 0.4$. Connection blue colour indicates positive correlations, red colour negative correlations. (C) Response of trait dimensions to a gradient of decreasing groundwater salinity and level (from left to right). Trait dimensions are the scores of the PC1 axes combining the highly correlated traits of the four groups shown in B. The solid lines show the community weighted means of these dimensions/modules on the salinity and groundwater depth gradient. The bands show convergence and divergence of the community weighted trait variance (FDvar) as a measure of functional diversity.

salinity reflecting decreasing tidal inundation frequency and duration from pioneer zones to upper saltmarshes, based on 62 plots on natural saltmarshes from the islands Mellum and Spiekeroog, Germany. Logistic regression models sorted species according to their fundamental abiotic niche requirements from left to right and according to their competitive abilities from right to left. This stress – competition sorting has been corroborated by multiple transplant experiments on saltmarshes (Crain et al. 2004). For each species, 15 traits were collected. These traits were to some extent all correlated and expressed as a trait correlation network (Fig. B1b). Cluster analysis and modularization techniques both identified four clusters or subnetworks of more strongly correlated traits in this correlation network ('seeds', 'salt tolerance', 'organ mass' and 'height'). The cluster 'seeds' can be associated with the movement dimension, the cluster 'salt tolerance' with the tolerance dimension and the two clusters organ mass and height with the interaction dimension (discussion in the Supporting information). Traits belonging to each cluster were aggregated with PCAs and the scores of the first PC axis used as four trait modules associated with the three dimensions. For each trait module and each plot, we calculated community-weighted means (CWM) and functional variance (FDvar). A regression with the groundwater depth and salinity gradient as predictor variable showed the investments to the dimensions and their convergence or divergence along the abiotic gradient with higher stress on the left side and stronger competition on the right side (Fig. B1c, details in the Supporting information).

The salt tolerance module representing the abiotic dimension showed increasing investments in mechanisms that increase salt tolerance towards high groundwater level and salinity (Fig. B1c). At both ends of the gradient, i.e. in the pioneer zone (left-hand side) and in the upper salt marsh (right-hand side), this module strongly converged around the mean whereas some divergence occurred at the lower salt marsh (centre). This coincides with the higher species diversity in the lower salt marsh, whereas the pioneer zone consists only of 3–4 salt tolerant species and the upper salt marsh of 1–3 salt sensitive species (Fig. B1a).

The seeds module representing the movement dimension decreased towards the upper salt marsh where the dominant species *Elytrigia atherica* (Supporting information) features few large seeds on each shoot (Supporting information). Conversely, species such as *Salicornia europaea* and *Suaeda maritima* occurring mainly in the pioneer zone produce many small seeds enabling good dispersal. However, *Spartina anglica*, also common in the pioneer zone, has few large seeds like *Elytrigia atherica* on the upper salt marsh. This leads to high divergence of the movement dimension towards high salinity and groundwater levels.

The organ mass and plant height modules representing the interaction dimension both increase and converge towards the more benign end of the gradient, as smaller plants are outcompeted in the upper salt marsh. In fact, the undisturbed upper salt marsh of the temperate Wadden Sea region is one of the few communities with monospecific stands of *Elytrigia atherica*. Towards increasing groundwater levels and higher salinity, we found higher divergence as plants with high organ masses and heights (e.g. *Atriplex portulacoides*, *Spartina anglica*) co-occur with smaller plants (e.g. *Salicornia* spp., *Puccinellia maritima*, *Spergularia maritima*). The mechanism enabling this coexistence is not yet fully understood.

Dimension means and variances in local community assembly

The tolerance dimension and related traits

Autotrophs form the basis of food webs on which plant–animal interactions can build (Li et al. 2018). At the beginning of a succession in an empty patch, community composition is driven by traits related to movement and abiotic filters, i.e. organisms must disperse to a potential habitat, but can only establish if their fundamental niche requirements match the abiotic conditions in this area (Soberón 2007). Investments of biomass or energy in traits associated with fundamental niche requirements constitute the tolerance dimension.

Traits associated with the tolerance dimension respond to environmental stress factors that limit species distributions irrespective of interactions with other species. These factors comprise living in water versus land, salinity, soil pH and most importantly, the climatic niche. Traits responding to these factors often determine macroecological distributions

in terrestrial, limnic or marine environments (Pinsky et al. 2019). Traits indicating climatic tolerance should converge across trophic levels as species whose trait expressions result in negative growth rates under a given climate cannot persist.

However, abiotic factors can also vary on very small spatial or temporal scales. An organism can experience a microclimate that may be quite different from the macroclimate. In salt marshes, soil salinity can increase seaward within a range of a few meters (Pennings et al. 2005). Correspondingly, investments in traits enabling tolerance to salinity increase, leading to convergence around high investments in the tolerance dimension (Fig. B1c).

Besides the niche given by fundamental abiotic factors related to species' physiological tolerances, the nutritional niche (Kearney et al. 2010) describes the resource availability required by a population to achieve a positive growth rate in the absence of competitors. The nutritional niche is part of the fundamental niche because no organism can survive in the (long-term) absence or too low availability of the diet it needs. This is particularly evident for animals requiring

specific dietary resources (e.g. oligolectic bees, specialist herbivores). When resources are available, sufficient acquisition can be hampered due to negative interactions with conspecifics and heterospecifics. Therefore, nutrition is part of both the tolerance and the interaction dimension. Nevertheless, the available amount of resources sets an upper boundary to the biomass or energy that can be invested to the three dimensions by a species. Therefore, we assess dimension means and variances separately for high and low resources.

Ecosystem engineers

Another aspect of the tolerance dimension is that traits enable species to modify their habitat by acting as ecosystem or habitat engineers (Corenblit et al. 2015). Ecosystem engineering encompasses all types of physical (e.g. bioturbation, sediment stabilization) and chemical (e.g. nitrification) habitat modification and formation (e.g. foundation species, symbioses; Jones et al. 1994). Recent studies have uncovered traits related to habitat engineering in land-sea transition zones. For example, Villnas et al. (2018) derived bioturbation potential for marine benthic invertebrates from body size and two qualitative organismal characteristics (sediment reworking mode and spatial location within or above the benthic layer). Another example of trait-related chemical habitat modification is the relationship between the structure of extracellular polymeric substances produced by benthic diatoms and the stability of the intertidal sediment (De Brouwer et al. 2005). Bouma et al. (2010) and Corenblit et al. (2015) reported plant traits such as stem stiffness that enable pioneer plants to colonize ecosystems at the land-water interface.

The interaction dimension and related traits

With increasing density of individuals, interactions intensify when superior competitors exclude others, feeding by consumers imposes top-down control in a food web or facilitation between species increases realized niches. In upper salt marshes, for instance, small annual plants with high fecundity, such as *Salicornia* spp., can rapidly colonize vacant patches but are displaced after a few years by perennial, rhizomatous and larger grasses such as *Elytrigia atherica* (Balke et al. 2017). Resource competition intensity depends on fitness inequalities among conspecifics and heterospecifics (Goldberg and Landa 1991) and associated traits. Here, we use the term fitness not in an evolutionary sense but as competitive ability (Mayfield and Levine 2010) or competitive advantage (Barabás et al. 2018). Relative fitness inequalities between species can originate from differences in space preemption and growth, fecundity or consumption rates of a shared resource (HilleRisLambers et al. 2012). Associated traits enable rapid growth rate, resource capture, space-filling and ultimately fecundity. In addition, fitness inequalities may be caused by differences in defenses against higher trophic level consumers (Brose 2008, Schneider et al. 2016) or pathogens (Lankau 2012). At the autotroph-herbivore interface, defense and morphological-phenological traits (Carmona et al. 2011, Deraison et al. 2015), stoichiometry (Klausmeier et al.

2004, Hillebrand et al. 2009) or other aspects of chemical (DeMott 1986, Pohnert et al. 2007, Van Donk et al. 2011, Rangel et al. 2016, Richards et al. 2016) and genomic composition (Guignard et al. 2016), are often proposed to influence interactions. Such traits can be used to construct functional network representations of the ecological interactions that organisms participate in, according to the framework of 'linkage rules' (Bartomeus et al. 2016, Delmas et al. 2019).

In practice, food-web studies have shown that body mass can drive trophic interactions (Warren and Lawton 1987, Brose et al. 2019). In this vein, optimal foraging models used allometric scaling of handling time and energy content to predict food-web structures (Beckerman et al. 2006, Thierry et al. 2011) and the likelihood of trophic links (Petchev et al. 2008, Ho et al. 2019). While body size and allometric relationships are still used as the most important predictors of food web links, particularly in aquatic food webs, it has become evident that trophic interactions are also driven by additional traits (Eklöf et al. 2013). For instance, the metabolic type and the movement mode of species that determine energetic demands and movement speed, respectively, have become the most likely additional trait dimensions (Hirt et al. 2020). Recently, trait-based linkage rules for trophic interactions have been extended to include the medium's physical properties in which predator and prey move, i.e. the tolerance dimension (Grady et al. 2019, Pawar et al. 2019, Portalier et al. 2019). Together, these studies demonstrate a complex interplay between species traits and the abiotic environment in driving trophic interactions.

Within trophic levels, coexistence of species is often mediated by competition for resources and space. Chesson's coexistence theory (Chesson 2003) is one of the leading frameworks in community ecology to understand multi-species coexistence as a result of processes that stabilize or equalize competitive outcomes among species (Barabás et al. 2018). Although the framework is not applicable to all kinds of interactions, we take it here as an example of how competitive processes may change interaction dimension means and variances. Specifically, we address 1) communities of species with almost equal competitive abilities, 2) communities of species with different competitive abilities stabilized by niche separation and 3) communities in which competitive hierarchies are equalized by resource pulses, disturbance or consumers (Fig. 2).

Equal competition

Species displacement occurs when relative fitness differences among heterospecifics exceed those among conspecifics (Hart et al. 2018). Displacement continues until competitive advantages among the remaining species are reduced to a level where the advantages are almost equal between heterospecifics and conspecifics. Equal competition leads to unstable species coexistence and neutral dynamics, often influenced by environmental stochasticity (Mcpeck and Siepielski 2019, Thompson et al. 2020), and to trait convergence in the interaction dimension (Fig. 2a, d: Equal competition; Grime 2006).

Stabilizing processes

Instead of continuous reduction towards equal competition, fitness inequalities can become stabilized by niche separation in time and space, among other processes (Barabás et al. 2018). Niche separation originates from differences in resource acquisition and resource conservation strategies among co-occurring species. Temporal niche separation is often based on different phenological growth strategies (Jensen et al. 2019). For instance, plant species that require large investments in maintenance and structural tissue, i.e. large stems, rhizomes and roots, are slow in growth while filling up an increasingly larger space. To co-occur, smaller plants must grow and reproduce faster before larger plants can fill the space, often by forgoing investments in large stems or root systems. Spatial niche separation can take place when a patch is spatially separated in several microsites (small-scale environmental heterogeneity) or vertical layers that can be exploited by organisms with different resource acquisition strategies (Schreier et al. 2009, HilleRisLambers et al. 2012, Donadi et al. 2015). Among sympatric animal species, niche separation is a cornerstone concept to understand competition avoidance (Hutchinson 1957, Schreier et al. 2009). For instance, animals can prevent niche overlap by temporal day–night separation in foraging or preying (Kronfeld-Schor et al. 2001). Waders foraging on intertidal mudflats and other water birds are a prime example of trait-based feeding niche separation, as differences in beak size, form and strength as well as leg length allow the exploitation of benthic macrofauna separated by soil depth, texture and water cover (Swennen et al. 1983, Henry and Cumming 2017). All in all, stabilized competition by niche separation should increase divergence in the interaction dimension among coexisting species (Fig. 2b, e).

Equalizing processes

Moderate periodical biomass removal by e.g. cutting, fire or erosion can break competitive hierarchies among species and equalize their competitive advantages and thus fitness differences, thereby preventing displacement of subordinate species and enhancing trait divergence (Kleyer 2002, Huston 2014). The strength of equalizing processes depends on the frequency, duration and magnitude of the disturbances on the one hand, and on the species' rates of regeneration and re-establishment of competitive ability on the other hand (White and Jentsch 2001, Gerlach et al. 2021). Besides disturbances, environmental stochasticity can create temporal fluctuations in resource supply that can equalize competitive advantages by favoring alternative resource acquisition strategies over time, resulting in divergence in the interaction dimension (Chesson et al. 2004). Yearly fluctuations in rainfall and temperature represent shifting resource supply points and can alternately favor species with different water and temperature requirements if both have some storage-effect in place that allows them to store reproductive capacity over unfavorable periods (Warner and Chesson 1985).

Consumer effects

Consumers can affect all three dimensions of lower trophic level communities. The tolerance dimension is easiest to understand: If a prey is defended against its predator – e.g. by secondary metabolites, active defense or capability for overcompensation-, then specialist predation will select for species that are well-defended. Some of the most well-known examples come from plant–herbivore systems. Large herbivores ('homogenous grazing'; Adler et al. 2001) mainly affect a plant's tolerance dimension by selecting only those species with rapid vegetative regeneration. Reduced grazing intensity can create spatiotemporal mosaics of ungrazed and intensively grazed patches (Kleyer et al. 2007), thus also creating mosaics of species with high and low tolerance to grazing, and hence plant communities whose composition is directly shaped by environmental filtering along the tolerance dimension.

In the interaction dimension, biotic filtering will occur whenever predation is frequency dependent – i.e. 1) each consumer preys upon a different prey (diet preferences), 2) predation depends on prey density or 3) there is spatial variation in consumer density, causing heterogeneity in prey communities (Pacala and Crawley 1992). Infrequent consumption can have equalizing or stabilizing effects on the species preyed on (Barabás et al. 2018), specifically when a keystone species selects prey with highly competitive traits in that community (Ryabov et al. 2015). If this trait is body mass and consumers prey on the species with the largest body mass, the dominance of these species can be broken and allow smaller species to coexist. This will lead to divergence in the interaction dimension at the lower trophic level (Fig. 2c, f: equalizing processes). For instance, moderately grazed upper saltmarshes are more trait-divergent than those ungrazed (Dupre and Diekmann 2001).

Finally, the movement dimension in prey communities is affected by consumers selecting for differences in prey mobility. One example is selective predation on weaker individuals (Pole et al. 2003). Similarly, dispersal traits can be selected for if consumer and/or prey dispersal rates affect coexistence (Shurin and Allen 2001).

There are multiple indirect interaction ways in which consumers can affect the dimension means and variances of lower trophic levels: 1) interaction modification and keystone predation, e.g. interactions at the plant level are modified by a herbivore that itself is affected by a predator (Calcagno et al. 2011); 2) symmetric or asymmetric apparent competition, e.g. consumers assert equal or differential pressures on lower trophic level species (Holt and Bonsall 2017) or 3) indirect mutualism, e.g. positive effects of one species on another species mediated by a consumer (Wootton 1994). These indirect interactions are not addressed here.

Hypotheses for the tolerance and interaction dimension in single communities

At the local scale, the tolerance and interaction dimensions respond to environmental gradients and successional time with changing means and variances. Here, we provide exemplary

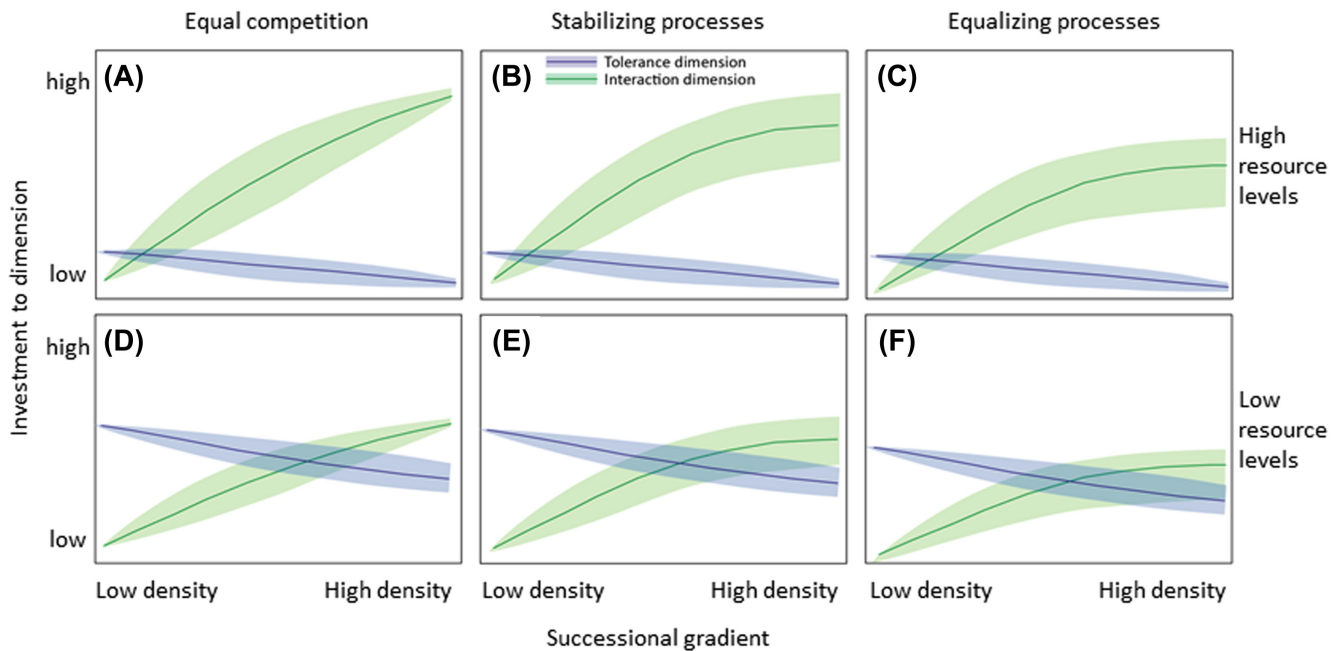


Figure 2. Hypothesized responses of the tolerance (blue) and interaction (green) dimension means and variances on a temporal successional gradient from low to high density for high (A–C) and low (D–F) resource levels and for equal (A, D), stabilizing (B, E) and equalizing (C, F) competition. Continuous lines: Community-weighted means of aggregated traits functionally associated with each dimension. Bands show the community-weighted functional variance around the mean.

hypotheses for sites with either high or low resource levels where density of individuals increases over time. An example of low resource levels and low density could be an initially vacant brownfield on soils with high gravel or sand content, whereas high resource levels and low density may stand for an arable field that was recently abandoned and then spontaneously colonised by plants and insects. Changes in dimensions are to some extent dependent on each other. When investments to one dimension increase, tradeoffs should lead to corresponding decreases in another dimension. This should apply to both community means and variances.

- 1) The overall investments allocated to dimensions are bounded by resource supply as organisms cannot invest more biomass or energy than they are able to acquire (Fig. 2a–c versus d–f).
- 2) On an almost vacant patch with low resources and few individuals, investments need to be allocated mainly to the tolerance dimension. With proceeding colonisation and increasing density, available resources need to be partitioned among more individuals. Conversely, higher density leads to higher resource mobilization, uptake and turn-over by decomposition, thus increasing the resource supply. Therefore, we predict slightly decreasing investments to the tolerance dimension when density increases (Fig. 2d–f). When early successional species facilitate more resources for later species and density increases, investments in the interaction dimension increase (Connell and Slatyer 1977)(Fig. 2a–f).
- 3) Under equal competition, the interaction dimension converges at high density (Fig. 2a, d), caused by the reduction

of the species pool to only those species that are similar in interaction (here: competition) traits. At this stage, intra- and interspecific competition is almost equal and the displacement rates of weaker competitors become exceedingly slow (Scheffer et al. 2018).

- 4) When stabilizing competition is present, such communities will, however, show divergence in the interaction dimension (Fig. 2b, e) because they niche-separate by using resources in different ways (Li et al. 2021).
- 5) Equalizing processes are often associated with non-selective biomass removal such as mowing or fire. This loss decreases the mean investment in the interaction dimension and increases its variance, when the dominance of competitive species is broken and subordinate species can prevail in the community (Fig. 2c, f; Biswas & Mallik 2010). For instance, plant size decreases when grassland communities are moderately grazed but the diversity of growth forms increase (McIntyre and Lavorel 2001).

Dimension means and variances in metacommunities

The movement dimension and related traits

To persist in fragmented landscapes with isolated habitats, species must track suitable habitat patches in space and time (Thomas 1994). They gain information about suitable habitats and each other at scales based on the resolution of their sensory organs and on their movement capacities (Portalier et al.

2019, Hein and Martin 2020, Hirt et al. 2020), making the movement dimension crucial for survival in fragmented landscapes (Kleyer et al. 2007). Movement of animals can be differentiated into dispersal, seasonal migration, home range and nomadism (review by Schlägel et al. 2020). Species that strongly interact within a given patch are those whose traits make their spatial scales of daily home range, foraging, orientation and spatial information processing overlapping. Traits related to movement larger than the daily foraging range, i.e. dispersal and migration, influence to what degree species couple communities spatially (Schleuning et al. 2020). For passively dispersed organisms, abiotic vectors need to be considered as well (e.g. wind, water currents; Ozinga et al. 2009).

Movement capability can vary greatly among the members of a community (Clobert et al. 2009). Hence, it may be more appropriate to consider the spatial dynamics and corresponding traits of the individual members of a community or guild instead of a community movement mean. If this resulted in too many individual spatial dynamics to be tractable, one might classify the species into separate movement groups based on shared movement traits. This contributes to the modular structure of food webs: animals with overlapping home ranges potentially strongly interact with each other, while animals with larger home ranges couple such strongly interacting modules into larger, modular food-webs (McCann et al. 2005). For example, seabirds with home ranges of up to 40 km couple marine and terrestrial food-webs by transporting nutrients between them (Hentati-Sundberg et al. 2020). Thus, these food webs become modules of a regional food-web.

Metacommunity-scale hypotheses

Based on the hypotheses for single local communities, we can predict the functional means and variances of each dimension along a gradient from high to low habitat isolation, subdivided by resource availability, equal or stabilized competition and finally low or high biomass removal by consumers (Fig. 3). In general, increasing divergence or convergence in one dimension should lead to a concomitant divergence or convergence in other dimensions, due to trait correlations between dimensions.

1) On the most isolated end of a spatiotemporal gradient, habitats are only reachable for species with high investments in traits of the movement dimension. Thus, communities in such habitats should show high convergence (low diversity) in that dimension (for plants: more, smaller seeds; for insects: larger wings or legs; Fig. 3). If the patches inhabited by these communities are small, most of the offspring will disperse to neighboring, unsuitable sites, thus draining reproductive capacity from the communities and possibly depleting diversity (source-sink dynamics and ecological traps; Pulliam 1988, Thompson et al. 2020). Local communities collectively form a metacommunity with heterogeneous community composition and asynchronous dynamics, due to infrequent colonization.

With decreasing isolation, the metacommunity changes to a single spatially structured community composed of local communities with a large exchange of individuals and strong interactions. This results in more homogenous species composition and coupled dynamics across all local communities. Average investments to the movement dimension decrease and diverge as species can reach the majority of all habitats regardless of their movement abilities (Fig. 3).

- 2) Good colonizers are often bad competitors because biomass investment to movement traits can trade off with investment to interaction traits, particularly when competitive ability is conferred by size (Hastings 1980, Leishman and Westoby 1994, Cadotte et al. 2006). Thus, good colonizers can inhabit spatially isolated patches, but are outcompeted in well-connected patches by good competitors (Mouquet and Loreau 2003, but see Parr and Gibb 2012), leading to a decrease in the movement dimension in non-isolated habitats (Fig. 3a). These exclusions lead to a spatially structured community of equally competing species characterized by a high and convergent interaction dimension (Fig. 3a), when high resources are not spatiotemporally separated within a patch and do not create spatial niche separation.
- 3) If resources and niches are separated and local communities are characterized by stabilizing competition, they will exhibit higher divergence in the interaction dimension and higher species richness (Fig. 3b; Thompson et al. 2020).
- 4) Low resource availability or high abiotic stress require more investments in the tolerance dimension (Fig. 3c). Species need to partition resources either to low growth rate, low movement and high endurance or to fast growth rate during periods of resource pulses and either escape or become dormant during unfavorable periods. At the high isolation corner of the gradient, allocation to the tolerance dimension trades off more strongly with allocation to the movement dimension as at the low isolation corner where species need to invest less to the movement dimension, but more to the interaction dimension. When movement investments decrease, the metacommunity may exhibit higher divergence in the trait-interaction dimension.
- 5) Increasing biomass removal by consumers does not strongly change the response of the dimension means to the isolation gradient, if these consumers are constrained by isolation in a similar way as their resource (Fig. 3d-f). At the well-connected end of the isolation gradient, local communities will, however, show a higher divergence of the trait-interaction dimension because competitive hierarchies between species will be equalized by the consumer. Non-selective consumers dispersing in a well-connected habitat network essentially act like equalizing factors across the whole metacommunity, preventing strong competitors from outcompeting other species. Consequently, the interaction dimension diverges stronger than on sites without biomass removal by consumers. Also, the movement dimension diverges because 1) bad

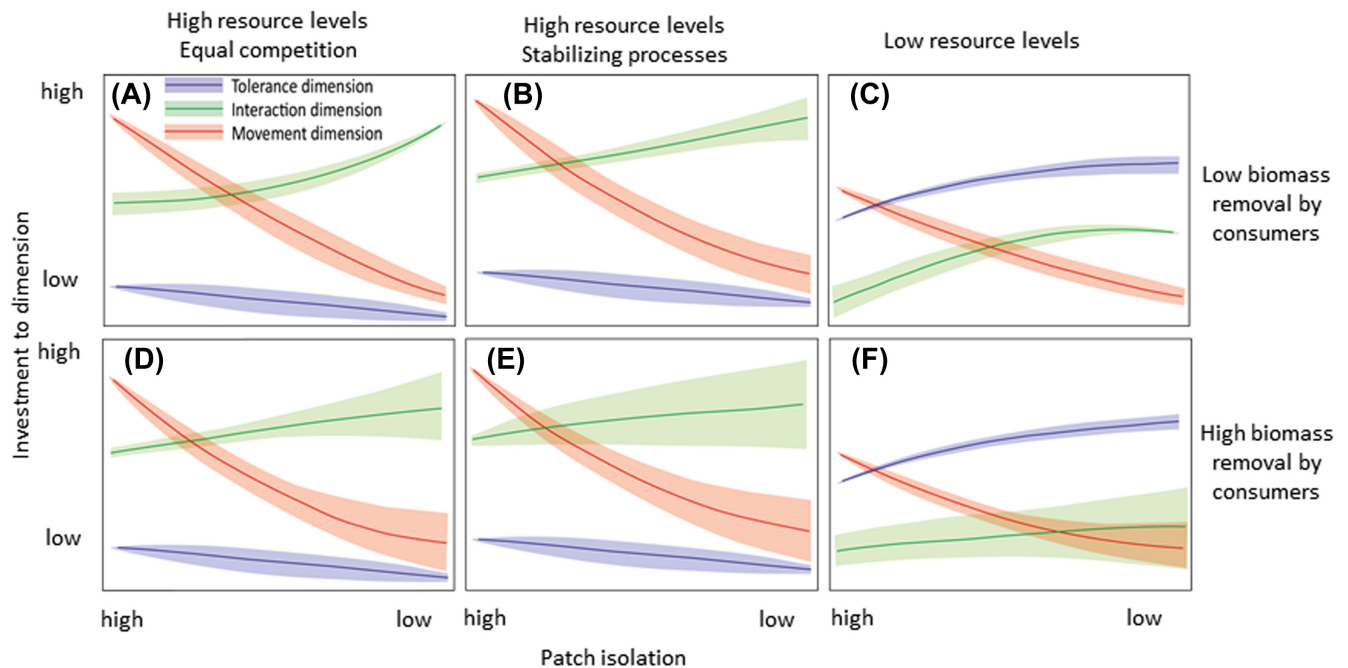


Figure 3. Predicted responses of tolerance, interaction and movement dimension means and variances on a patch isolation gradient for high (A, B, D, E) and low (C, F) resource availability, equal (A, D) and stabilized competition, and low (D–F) and high (A–C) biomass removal by a consumer. These predictions are applicable to a community of producers interacting with a single trophic level of generalist consumers that are constrained by isolation in the same way as the producers. Continuous lines: Community-weighted means of aggregated traits functionally associated with each dimension. Bands show the community-weighted functional variance around the mean.

competitors, being released from competitive pressure, can be better colonizers (Guzman et al. 2019) or 2) organisms are favored that can better escape consumer pressure. Consumers specialized on weak competitors in the lower trophic level can, however, increase the extinction risk of such species, thus decreasing functional diversity at this lower level.

- 6) With environmental stress or limited resources, the decreased effect of a consumer may result from a reduced spatio-temporal match with its prey (Durant et al. 2005, Doiron et al. 2015). This may cause a similar interaction divergence of the lower trophic level at the more isolated edge of the isolation gradient (Fig. 3f), as if biomass removal by a consumer were low (Fig. 3c).

Dimension means and variances can differ between a single community and the metacommunity scale. Small-scale environmental stochasticity or disturbances as well as genetic and demographic stochasticity can lead to species extinctions at the local scale, whereas large-scale, spatially correlated environmental stochasticity can synchronize whole metacommunity dynamics (Moran effect; Ranta et al. 1997, Liebhold et al. 2004). In some patches, populations can be rescued when dispersing individuals reach the patches and re-establish within the community of the resident species (Louette et al. 2008, Schleicher et al. 2011). The resulting random heterogeneity in species composition will be reflected in random trait variation, increasing the overall variation at the metacommunity scale.

The hypotheses cover changes of dimension means and variances within a single trophic level and across two levels. Including even higher trophic levels may change these hypotheses (Godoy et al. 2018, Guzman et al. 2019). These changes depend on transfer efficiencies among trophic levels (Barbier and Loreau 2019). Also, trophic dynamics can be cyclic, which would mean constant shifts in community trait distributions based on changes in the selective landscape (Tirok et al. 2011, Bauer et al. 2014). Thus, our hypotheses on trait distributions are valid only for coarser time scales than cycle lengths of food web dynamics.

Discussion and future directions

Our framework is an integrative approach that attempts to advance a functional metacommunity ecology. It obviously is only a step towards achieving a consistent body of theory and empiricism. However, as argued above, it holds both the generality and flexibility needed to be applicable to a wide range of real-world examples. Here we discuss both advantages and caveats of this approach as well as anticipated developments. As space permits only a subset of the many directions, we address 1) dimensions as broad generalizations of multiple functions, 2) functional trait analogues, 3) relationships between dimensions as well as responses to and effects on meta-ecosystems (Loreau et al. 2003) and finally 4) functional dimension matching between trophic levels.

1) Tolerance, interaction and movement dimensions as broad generalizations of multiple functions

The tolerance, interaction and movement dimensions are strong simplifications of real trait network changes along gradients, as they were designed to overcome trait differences between autotrophs and heterotrophs organized in food webs. Obviously, each dimension can be differentiated into subcategories addressing specific functions. For instance, Guzman et al. (2019) separated movement into dispersal, migration, foraging and spatial information processing, each with potentially different effects on metacommunity dynamics and food web coupling. Thus, our framework is not meant to be an authoritative classification valid in all contexts, but rather a tool to encourage systematic thinking about multiple ecological processes being affected by community trait distributions. We see strong potential in using these dimensions to unify empirical and theoretical metacommunity ecology. The development of metacommunity models has been fast and outpaced the empirical assessments (Logue et al. 2011), as the modelled processes are not easily measurable in the field, and measured traits are not directly linked to modelled traits. Our proposal will help to close this gap by mapping traits on three dimensions, which reflect the core metacommunity ingredients movement/dispersal, niche/species sorting and interactions. A next logical step would be to transfer our hypotheses into a mathematical framework to derive quantitative hypotheses for the relative investment in different dimensions. This ‘investment’, however, is a caveat of our approach, as its definition, measurement and incorporation in models requires more research and synthesis (but see Sokolova 2021). When dimensions are associated with certain organs such as movement to wings or legs, the allocated biomass to these organs can be relatively easily measured. More research and synthesis are needed when ‘investments’ are less easily measurable, such as information processing abilities in different taxa. While behavior, sensory abilities and orientation skills are crucial for the movement and interaction dimension, lack of information on their effects prevents their inclusion in models and empirical studies (Kingsford et al. 2002, Mouritsen 2018). On the other hand, investment is key to highly mechanistic models such as dynamic energy budget theory (Kooijman 2010) or ecological stoichiometry (Sternner and Elser 2002), which potentially allow to connect from physiology to spatial ecology.

2) Functional analogues

The development of functional trophic metacommunity ecology is strongly hampered by the obvious differences between traits of different taxa, such as marine or terrestrial autotrophs and heterotrophs. How could we calculate trait means and variances across taxa that do not share the same traits? This can be even difficult in plants when stems of rushes are functional equivalents to leaves of other plants for carbon fixation. Weiss and Ray (2019) introduced the concept of functional analogues, i.e. traits that are comparable between taxa

in capturing ‘both the relevant ecological phenomena and the relevant community assembly process(es) studied’ (Weiss and Ray 2019, p. 2014). Functional analogues are made comparable once they are converted to the same performance currencies using mathematical relationships (McGill et al. 2006). More research is needed regarding cross-taxa functional trait comparisons and the scales on which they are feasible.

3) Relationships between dimensions in meta-ecosystems

Instead of addressing single traits as independent entities, research should focus on the relationships among traits (Messier et al. 2017) and ultimately trait positions on tradeoff and allometric landscapes in response to abiotic, interaction and movement constraints. This would require trait measurements of many species across major taxonomic groups, based on the concept of functional analogues. To assess the strength of trait covariances it is important to measure traits of different dimensions on the same individual (Westoby et al. 2002, Kleyer and Minden 2015). With improved knowledge of trait correlations available, an important future research question is in how far environmental pressure acting on a single dimension propagates through the whole network of traits and dimensions as a result of the connectedness of the traits in the network. Depending on trait connectedness, the dimension under selection by a consumer may affect multiple other traits and either change the whole phenotype or just a single organ. For instance, cattle select plant stem lengths large enough to be torn away by their tongues, leading to decreased size of the remaining plants. As stem mass is strongly correlated with root mass, reproductive mass and many other traits, regular grazing affects the whole plant phenotype (Kleyer et al. 2019). If this is considered in a trophic framework, we can envisage trait networks of a certain trophic level, e.g. autotrophs, affected by another trophic level, e.g. a guild of consumers, which in itself represents a network of traits. An interesting question is then to understand how the interaction propagates through both networks, by not only affecting the matching traits, but through their links to other traits. Again, phenotypes may change as a whole or only in specific organ traits, such as specific leaf area or beak shape.

4) Improve knowledge on trait matching between trophic levels

We hypothesized that the strength of trophic interaction between lower trophic levels and consumers leads to divergence in the competition traits at the lower trophic level. Albrecht et al. (2018) showed that the top-down control of trait divergence can also have repercussions on the interaction diversity of the upper trophic level, i.e. bottom-up and top-down effects may simultaneously control the assembly of plant-animal interaction networks. The connectedness of these networks relies on the matching of species’ traits across taxa (Schleuning et al. 2015, Bartomeus et al. 2016). The matching of resource use traits of consumers and defence

traits of resources are expected to affect 1) trophic interaction probabilities (i.e. diets), 2) consumer responses to variation in the amount of prey or resources or 3) the effect of consumers on resource densities. A similar reasoning applies to mutualism-related traits, e.g. pollination-related traits. Finally, traits related to habitat engineering are hypothesized to affect the efficiency of different organisms to affect abiotic conditions. More research is needed on whether matching of species' traits across taxa only imply the interaction dimension or also act across dimensions. For example, movement and interaction are directly related in, e.g. the case of animal-dispersed plants in which the number of fruits eaten can be directly converted into number of seeds dispersed that have passed the digestive tract unharmed while the animal moved (Morán-López et al. 2020).

Conclusions

A metacommunity theory rooted in trait-based and multi-trophic principles is not yet achieved. After decades of research, the relationships between functional traits and community-level patterns remain complex, particularly when communities are structured in space and time across trophic levels. Further studies are needed that compare traits associated with the tolerance, interaction and movement dimensions across taxa and across different habitats and marine and terrestrial environments. As a heuristic tool, we presented hypotheses to steer such studies. We have also shown that processes falling under these dimensions can be linked to empirically measurable traits organized in trait networks (Box 1). Importantly, not all dimensions are equally well investigated. For instance, more quantitative studies linking functional traits to niche construction processes are needed. Nevertheless, functional trait research has made much progress in identifying traits that are both good predictors of functionality and empirically obtainable at reasonable costs. Now the time is ripe for the integration of functional trait research across taxa and ecosystems to inform studies aiming to describe and understand changes in metacommunity composition and interaction networks in response to environmental change.

Acknowledgements – We thank the subject editor Dominique Gravel and the reviewers for their comments that helped us to improve the manuscript.

Funding – The authors acknowledge funding by the German Science Foundation to the DynaCom project (Spatial community ecology in highly dynamic landscapes: from island biogeography to metaecosystems) as Research Unit number FOR 2716.

Author contributions

Barbara Bauer: Conceptualization (equal); Writing – original draft (lead); Writing – review and editing (equal). **Michael Kleyer:** Conceptualization (equal); Writing – original draft (supporting); Writing – review and editing (lead). **Dirk C. Albach:** Writing – original draft (supporting); Writing – review and

editing (equal). **Bernd Blasius:** Writing – original draft (supporting); Writing – review and editing (equal). **Ulrich Brose:** Conceptualization (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Thalita Ferreira-Arruda:** Writing – original draft (supporting); Writing – review and editing (equal). **Ulrike Feudel:** Writing – original draft (supporting); Writing – review and editing (equal). **Gabriele Gerlach:** Writing – original draft (supporting); Writing – review and editing (equal). **Christian Hof:** Writing – original draft (supporting); Writing – review and editing (equal). **Holger KrefT:** Writing – original draft (supporting); Writing – review and editing (equal). **Lucie Kuczynski:** Writing – review and editing (equal). **Kertu Lóhmus:** Writing – review and editing (equal). **Stefanie Moorthi:** Writing – original draft (supporting); Writing – review and editing (equal). **Christoph Scherber:** Writing – original draft (supporting); Writing – review and editing (equal). **Stefan Scheu:** Writing – original draft (supporting); Writing – review and editing (equal). **Gerhard Zotz:** Writing – original draft (supporting); Writing – review and editing (equal). **Helmut Hillebrand:** Conceptualization (equal); Writing – original draft (supporting); Writing – review and editing (equal).

Data availability statement

This paper contains no original data.

References

- Adler, P. B. et al. 2001. The effect of grazing on the spatial heterogeneity of vegetation. – *Oecologia* 128: 465–479.
- Albrecht, J. et al. 2018. Plant and animal functional diversity drive mutualistic network assembly across an elevational gradient. – *Nat. Commun.* 9: 3177.
- Balke, T. et al. 2017. Experimental salt marsh islands: a model system for novel metacommunity experiments. – *Estuar. Coast. Shelf Sci.* 198: 288–298.
- Barabás, G. et al. 2018. Chesson's coexistence theory. – *Ecol. Monogr.* 88: 277–303.
- Barbier, M. and Loreau, M. 2019. Pyramids and cascades: a synthesis of food chain functioning and stability. – *Ecol. Lett.* 22: 405–419.
- Bartomeus, I. et al. 2016. A common framework for identifying linkage rules across different types of interactions. – *Funct. Ecol.* 30: 1894–1903.
- Bauer, B. et al. 2014. Diversity, functional similarity and top-down control drive synchronization and the reliability of ecosystem function. – *Am. Nat.* 183: 394–409.
- Beckerman, A. P. et al. 2006. Foraging biology predicts food web complexity. – *Proc. Natl Acad. Sci. USA* 103: 13745–13749.
- Biswas, S. R. and Mallik, A. U. 2010. Disturbance effects on species diversity and functional diversity in riparian and upland plant communities. – *Ecology* 91: 28–35.
- Bouma, T. J. et al. 2010. Comparing ecosystem engineering efficiency of two plant species with contrasting growth strategies. – *Ecology* 91: 2696–2704.
- Brose, U. 2008. Complex food webs prevent competitive exclusion among producer species. – *Proc. R. Soc. B* 275: 2507–2514.

- Brose, U. and Hillebrand, H. 2016. Biodiversity and ecosystem functioning in dynamic landscapes. – *Phil. Trans. R. Soc. B* 371: 20150267.
- Brose, U. et al. 2019. Predator traits determine food-web architecture across ecosystems. – *Nat. Ecol. Evol.* 3: 919–927.
- Brousseau, P. M. et al. 2018. On the development of a predictive functional trait approach for studying terrestrial arthropods. – *J. Anim. Ecol.* 87: 1209–1220.
- Burns, K. C. and Neufeld, C. J. 2009. Plant extinction dynamics in an insular metacommunity. – *Oikos* 118: 191–198.
- Cadotte, M. W. et al. 2006. On testing the competition–colonization tradeoff in a multispecies assemblage. – *Am. Nat.* 168: 704–709.
- Calcagno, V. et al. 2011. Keystone predation and plant species coexistence: the role of carnivore hunting mode. – *Am. Nat.* 177: E1–E13.
- Carmona, D. et al. 2011. Plant traits that predict resistance to herbivores. – *Funct. Ecol.* 25: 358–367.
- Chesson, P. 2003. Quantifying and testing coexistence mechanisms arising from recruitment fluctuations. – *Theor. Pop. Biol.* 64: 345–357.
- Chesson, P. et al. 2004. Resource pulses, species interactions and diversity maintenance in arid and semi-arid environments. – *Oecologia* 141: 236–253.
- Clobert, J. et al. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. – *Ecol. Lett.* 12: 197–209.
- Connell, J. H. and Slatyer, R. O. 1977. Mechanisms of succession in natural communities and their role in community stability and organisation. – *Am. Nat.* 111: 1119–1144.
- Corenblit, D. et al. 2015. Engineer pioneer plants respond to and affect geomorphic constraints similarly along water–terrestrial interfaces world-wide. – *Global Ecol. Biogeogr.* 24: 1363–1376.
- Crain, C. M. et al. 2004. Physical and biotic drivers of plant distribution across estuarine salinity gradients. – *Ecology* 85: 2539–2549.
- De Brouwer, J. F. C. et al. 2005. Biogenic stabilization of intertidal sediments: the importance of extracellular polymeric substances produced by benthic diatoms. – *Microb. Ecol.* 49: 501–512.
- Delmas, E. et al. 2019. Analysing ecological networks of species interactions. – *Biol. Rev.* 94: 16–36.
- DeMott, W. R. 1986. The role of taste in food selection by freshwater zooplankton. – *Oecologia* 69: 334–340.
- Deraison, H. et al. 2015. Functional trait diversity across trophic levels determines herbivore impact on plant community biomass. – *Ecol. Lett.* 18: 1346–1355.
- Diaz, S. et al. 1998. Plant functional traits and environmental filters at a regional scale. – *J. Veg. Sci.* 9: 113–122.
- Doiron, M. et al. 2015. Trophic mismatch and its effects on the growth of young in an Arctic herbivore. – *Global Change Biol.* 21: 4364–4376.
- Donadi, S. et al. 2015. Multi-scale habitat modification by coexisting ecosystem engineers drives spatial separation of macrobenthic functional groups. – *Oikos* 124: 1502–1510.
- Dupre, C. and Diekmann, M. 2001. Differences in species richness and life-history traits between grazed and abandoned grasslands in southern Sweden. – *Ecography* 24: 275–286.
- Durant, J. M. et al. 2005. Timing and abundance as key mechanisms affecting trophic interactions in variable environments. – *Ecol. Lett.* 8: 952–958.
- Eklöf, A. et al. 2013. The dimensionality of ecological networks. – *Ecol. Lett.* 16: 577–583.
- Garnier, E. et al. 2007. Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. – *Ann. Bot.* 99: 967–985.
- Gerlach, G. et al. 2021. Impact of cyclones on hard coral and meta-population structure, connectivity and genetic diversity of coral reef fish. – *Coral Reefs*, doi: 10.1007/s00338-021-02096-9.
- Godoy, O. et al. 2018. Towards the integration of niche and network theories. – *Trends Ecol. Evol.* 33: 287–300.
- Goldberg, D. E. and Landa, K. 1991. Competitive effect and response: hierarchies and correlated traits in the early stages of competition. – *J. Ecol.* 79: 1013–1030.
- Grady, J. M. et al. 2019. Metabolic asymmetry and the global diversity of marine predators. – *Science* 363: eaat4220.
- Gravel, D. et al. 2011. Trophic theory of island biogeography. – *Ecol. Lett.* 14: 1010–1016.
- Gravel, D. et al. 2016. The meaning of functional trait composition of food webs for ecosystem functioning. – *Phil. Trans. R. Soc. B* 371: 20150268.
- Grime, J. P. 2002. Plant strategies, vegetation processes and ecosystem properties. – Wiley.
- Grime, J. P. 2006. Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. – *J. Veg. Sci.* 17: 255–260.
- Guignard, M. S. et al. 2016. Genome size and ploidy influence angiosperm species' biomass under nitrogen and phosphorus limitation. – *New Phytol.* 210: 1195–1206.
- Guzman, L. M. et al. 2019. Towards a multi-trophic extension of metacommunity ecology. – *Ecol. Lett.* 22: 19–33.
- Hart, S. P. et al. 2018. How to quantify competitive ability. – *J. Ecol.* 106: 1902–1909.
- Hastings, A. 1980. Disturbance, coexistence, history and competition for space. – *Theor. Popul. Biol.* 18: 363–373.
- Hein, A. M. and Martin, B. T. 2020. Information limitation and the dynamics of coupled ecological systems. – *Nat. Ecol. Evol.* 4: 82–90.
- Heino, J. et al. 2015. Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. – *Freshwater Biol.* 60: 845–869.
- Henry, D. A. W. and Cumming, G. S. 2017. Can waterbirds with different movement, dietary and foraging functional traits occupy similar ecological niches? – *Landscape Ecol.* 32: 265–278.
- Hentati-Sundberg, J. et al. 2020. Fueling of a marine–terrestrial ecosystem by a major seabird colony. – *Sci. Rep.* 10: 15455.
- Hillebrand, H. et al. 2009. Herbivore metabolism and stoichiometry each constrain herbivory at different organizational scales across ecosystems. – *Ecol. Lett.* 12: 516–527.
- HilleRisLambers, J. et al. 2012. Rethinking community assembly through the lens of coexistence theory. – *Annu. Rev. Ecol. Evol. Syst.* 43: 227–248.
- Hirt, M. R. et al. 2020. Rethinking trophic niches: speed and body mass colimit prey space of mammalian predators. – *Ecol. Evol.* 10: 7094–7105.
- Ho, H. C. et al. 2019. Predation risk influences food-web structure by constraining species diet choice. – *Ecol. Lett.* 22: 1734–1745.
- Holt, R. D. and Bonsall, M. B. 2017. Apparent competition. – *Annu. Rev. Ecol. Evol. Syst.* 48: 447–471.
- Huston, M. A. 2014. Disturbance, productivity and species diversity: empiricism vs. logic in ecological theory. – *Ecology* 95: 2382–2396.
- Hutchinson, G. E. 1957. Concluding remarks. – *Cold Spring Harb. Symp. Quant. Biol.* 22: 415–427.

- Jacquet, C. et al. 2017. Extensions of Island biogeography theory predict the scaling of functional trait composition with habitat area and isolation. – *Ecol. Lett.* 20: 135–146.
- Jeliaskov, A. et al. 2020. A global database for metacommunity ecology, integrating species, traits, environment and space. – *Sci. Data* 7: 6.
- Jensen, A. M. et al. 2019. Evidence of temporal niche separation via low flowering time overlap in an old-field plant community. – *Oecologia* 189: 1071–1082.
- Jones, C. G. et al. 1994. Organisms as ecosystem engineers. – *Oikos* 69: 373–386.
- Kearney, M. et al. 2010. Modelling the ecological niche from functional traits. – *Phil. Trans. R. Soc. B* 365: 3469–3483.
- Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. – *J. Veg. Sci.* 3: 157–164.
- Kingsford, M. J. et al. 2002. Sensory environments, larval abilities and local self-recruitment. – *Bull. Mar. Sci.* 70: 309–340.
- Kjørboe, T. 2011. How zooplankton feed: mechanisms, traits and trade-offs. – *Biol. Rev.* 86: 311–339.
- Klausmeier, C. A. et al. 2004. Optimal nitrogen-to-phosphorus stoichiometry of phytoplankton. – *Nature* 429: 171–174.
- Kleyer, M. 2002. Validation of plant functional types across two contrasting landscapes. – *J. Veg. Sci.* 13: 167–178.
- Kleyer, M. and Minden, V. 2015. Why functional ecology should consider all plant organs: an allocation-based perspective. – *Basic Appl. Ecol.* 16: 1–9.
- Kleyer, M. et al. 2007. Mosaic cycles in agricultural landscapes of northwest Europe. – *Basic Appl. Ecol.* 8: 295–309.
- Kleyer, M. et al. 2019. Trait correlation network analysis identifies biomass allocation traits and stem specific length as hub traits in herbaceous perennial plants. – *J. Ecol.* 107: 829–842.
- Kneitel, J. M. and Chase, J. M. 2004. Tradeoffs in community ecology: linking spatial scales and species coexistence. – *Ecol. Lett.* 7: 69–80.
- Kooijman, S. A. L. M. 2010. Dynamic energy budget theory for metabolic organisation. – Cambridge Univ. Press.
- Kronfeld-Schor, N. et al. 2001. On the use of the time axis for ecological separation: diel rhythms as an evolutionary constraint. – *Am. Nat.* 158: 451–457.
- Lankau, R. A. 2012. Coevolution between invasive and native plants driven by chemical competition and soil biota. – *Proc. Natl Acad. Sci. USA* 109: 11240–11245.
- Leibold, M. A. et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. – *Ecol. Lett.* 7: 601–613.
- Leishman, M. R. and Westoby, M. 1994. The role of large seed size in shaded conditions: experimental evidence. – *Funct. Ecol.* 8: 205–214.
- Letten, A. D. et al. 2017. Linking modern coexistence theory and contemporary niche theory. – *Ecol. Monogr.* 87: 161–177.
- Li, D. et al. 2018. Homogenization of species composition and species association networks are decoupled. – *Global Ecol. Biogeogr.* 27: 1481–1491.
- Li, X. et al. 2021. Leaf plasticity contributes to plant anti-herbivore defenses and indicates selective foraging: implications for sustainable grazing. – *Ecol. Indic.* 122: 107273.
- Liebold, A. et al. 2004. Spatial synchrony in population dynamics. – *Annu. Rev. Ecol. Evol. Syst.* 35: 467–490.
- Logue, J. B. et al. 2011. Empirical approaches to metacommunities: a review and comparison with theory. – *Trends Ecol. Evol.* 26: 482–491.
- Loreau, M. et al. 2003. Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. – *Ecol. Lett.* 6: 673–679.
- Louette, G. et al. 2008. Assembly of zooplankton communities in newly created ponds. – *Freshwater Biol.* 53: 2309–2320.
- Mayfield, M. M. and Levine, J. M. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. – *Ecol. Lett.* 13: 1085–1093.
- McCann, K. S. et al. 2005. The dynamics of spatially coupled food webs. – *Ecol. Lett.* 8: 513–523.
- McGill, B. J. et al. 2006. Rebuilding community ecology from functional traits. – *Trends Ecol. Evol.* 21: 178–185.
- McIntyre, S. and Lavorel, S. 2001. Livestock grazing in subtropical pastures: steps in the analysis of attribute response and plant functional types. – *J. Ecol.* 89: 209–226.
- Mcpeek, M. A. and Siepielski, A. M. 2019. Disentangling ecologically equivalent from neutral species: the mechanisms of population regulation matter. – *J. Anim. Ecol.* 88: 1755–1765.
- Messier, J. et al. 2017. Interspecific integration of trait dimensions at local scales: the plant phenotype as an integrated network. – *J. Ecol.* 105: 1775–1790.
- Morán-López, T. et al. 2020. Can network metrics predict vulnerability and species roles in bird-dispersed plant communities? Not without behaviour. – *Ecol. Lett.* 23: 348–358.
- Mouquet, N. and Loreau, M. 2003. Community patterns in source-sink metacommunities. – *Am. Nat.* 162: 544–557.
- Mouritsen, H. 2018. Long-distance navigation and magnetoreception in migratory animals. – *Nature* 558: 50–59.
- Obeso, J. R. 2002. The costs of reproduction in plants. – *New Phytol.* 155: 321–348.
- Ozinga, W. A. et al. 2009. Dispersal failure contributes to plant losses in NW Europe. – *Ecol. Lett.* 12: 66–74.
- Pacala, S. W. and Crawley, M. J. 1992. Herbivores and plant diversity. – *Am. Nat.* 140: 243–260.
- Parr, C. L. and Gibb, H. 2012. The discovery–dominance tradeoff is the exception, rather than the rule. – *J. Anim. Ecol.* 81: 233–241.
- Pawar, S. et al. 2019. Interaction dimensionality scales up to generate bimodal consumer–resource size-ratio distributions in ecological communities. – *Front. Ecol. Evol.* 7: 1–11.
- Pennings, S. C. et al. 2005. Plant zonation in low-latitude salt marshes: disentangling the roles of flooding, salinity and competition. – *J. Ecol.* 93: 159–167.
- Petchev, O. L. et al. 2008. Size, foraging and food web structure. – *Proc. Natl Acad. Sci. USA* 105: 4191–4196.
- Pillai, P. et al. 2011. Metacommunity theory explains the emergence of food web complexity. – *Proc. Natl Acad. Sci. USA* 108: 19293–19298.
- Pinsky, M. L. et al. 2019. Greater vulnerability to warming of marine versus terrestrial ectotherms. – *Nature* 569: 108–111.
- Pohnert, G. et al. 2007. Chemical cues, defence metabolites and the shaping of pelagic interspecific interactions. – *Trends Ecol. Evol.* 22: 198–204.
- Pole A et al. 2003. African wild dogs test the ‘survival of the fittest’ paradigm. – *Proc. R. Soc. B* 270: S57.
- Portalier, S. M. J. et al. 2019. The mechanics of predator–prey interactions: first principles of physics predict predator–prey size ratios. – *Funct. Ecol.* 33: 323–334.
- Pulliam, H. R. 1988. Sources, sinks and population regulation. – *Am. Nat.* 132: 652–661.
- Rangel, L. M. et al. 2016. Toxicity overrides morphology on *Cylindrospermopsis raciborskii* grazing resistance to the calanoid copepod *Eudiaptomus gracilis*. – *Microb. Ecol.* 71: 835–844.
- Ranta, E. et al. 1997. The Moran effect and synchrony in population dynamics. – *Oikos* 78: 136–142.

- Richards, L. A. et al. 2016. Phytochemical diversity and synergistic effects on herbivores. – *Phytochem. Rev.* 15: 1153–1166.
- Ryabov, A. B. et al. 2015. Imperfect prey selectivity of predators promotes biodiversity and irregularity in food webs. – *Ecol. Lett.* 18: 1262–1269.
- Scheffer, M. et al. 2018. Toward a unifying theory of biodiversity. – *Proc. Natl Acad. Sci. USA* 115: 639–641.
- Schlägel, U. E. et al. 2020. Movement-mediated community assembly and coexistence. – *Biol. Rev.* 95: 1073–1096.
- Schleicher, A. et al. 2011. Dispersal traits determine plant response to habitat connectivity in an urban landscape. – *Landscape Ecol.* 26: 529–540.
- Schleuning, M. et al. 2014. Ecological, historical and evolutionary determinants of modularity in weighted seed-dispersal networks. – *Ecol. Lett.* 17: 454–463.
- Schleuning, M. et al. 2015. Predicting ecosystem functions from biodiversity and mutualistic networks: an extension of trait-based concepts to plant–animal interactions. – *Ecography* 38: 380–392.
- Schleuning, M. et al. 2020. Trait-based assessments of climate-change impacts on interacting species. – *Trends Ecol. Evol.* 35: 319–328.
- Schneider, F. D. et al. 2016. Animal diversity and ecosystem functioning in dynamic food webs. – *Nat. Commun.* 7: 12718.
- Schoener, T. W. 1986. Mechanistic approaches to community ecology: a new reductionism. – *Integr. Comp. Biol.* 26: 81–106.
- Schreier, B. M. et al. 2009. Interspecific competition and niche separation in primates: a global analysis. – *Biotropica* 41: 283–291.
- Shoemaker, L. G. and Melbourne, B. A. 2016. Linking metacommunity paradigms to spatial coexistence mechanisms. – *Ecology* 97: 2436–2446.
- Shurin, J. B. and Allen, E. G. 2001. Effects of competition, predation and dispersal on species richness at local and regional scales. – *Am. Nat.* 158: 624–637.
- Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. – *Ecol. Lett.* 10: 1115–1123.
- Sokolova, I. 2021. Bioenergetics in environmental adaptation and stress tolerance of aquatic ectotherms: linking physiology and ecology in a multi-stressor landscape. – *J. Exp. Biol.* 224: jeb236802.
- Spasojevic, M. J. and Suding, K. N. 2011. Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. – *J. Ecol.* 100: 652–661.
- Staniczenko, P. P. A. et al. 2017. Linking macroecology and community ecology: refining predictions of species distributions using biotic interaction networks. – *Ecol. Lett.* 20: 693–707.
- Stearns, S. C. 1989. Trade-offs in life-history evolution. – *Funct. Ecol.* 3: 259–268.
- Sturner, R. W. and Elser, J. 2002. Ecological stoichiometry. The biology of elements from molecules to the biosphere. – Princeton Univ. Press.
- Swennen, C. et al. 1983. Differences in bill form of the oystercatcher *Haematopus ostralegus*; a dynamic adaptation to specific foraging techniques. – *Neth. J. Sea Res.* 17: 57–83.
- Thierry, A. et al. 2011. The consequences of size dependent foraging for food web topology. – *Oikos* 120: 493–502.
- Thomas, C. D. 1994. Extinction, colonization and metapopulations – environmental tracking by rare species. – *Cons. Biol.* 8: 373–378.
- Thompson, P. L. et al. 2020. A process-based metacommunity framework linking local and regional scale community ecology. – *Ecol. Lett.* 23: 1314–1329.
- Tirok, K. et al. 2011. Predator–prey dynamics driven by feedback between functionally diverse trophic levels. – *PLoS One* 6: e27357.
- Van Donk, E. et al. 2011. Induced defences in marine and freshwater phytoplankton: a review. – *Hydrobiologia* 668: 3–19.
- Villnas, A. et al. 2018. Template for using biological trait groupings when exploring large-scale variation in seafloor multifunctionality. – *Ecol. Appl.* 28: 78–94.
- Violle, C. et al. 2007. Let the concept of trait be functional! – *Oikos* 116: 882–892.
- Wang, S. and Loreau, M. 2016. Biodiversity and ecosystem stability across scales in metacommunities. – *Ecol. Lett.* 19: 510–518.
- Warner, R. R. and Chesson, P. L. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. – *Am. Nat.* 125: 769.
- Warren, P. H. and Lawton, J. H. 1987. Invertebrate predator–prey body size relationships: an explanation for upper triangular food webs and patterns in food web structure? – *Oecologia* 74: 231–235.
- Weiher, E. and Keddy, P. A. 1995. The assembly of experimental wetland plant-communities. – *Oikos* 73: 323–335.
- Weiher, E. et al. 2011. Advances, challenges and a developing synthesis of ecological community assembly theory. – *Phil. Trans. R. Soc. B* 366: 2403–2413.
- Weiner, J. 2004. Allocation, plasticity and allometry in plants. – *Perspect. Plant Ecol. Evol. Syst.* 6: 207–215.
- Weiss, K. C. B. and Ray, C. A. 2019. Unifying functional trait approaches to understand the assemblage of ecological communities: synthesizing taxonomic divides. – *Ecography* 42: 2012–2020.
- Westoby, M. et al. 2002. Plant ecological strategies: some leading dimensions of variation between species. – *Annu. Rev. Ecol. Syst.* 33: 125–159.
- White, P. S. and Jentsch, A. 2001. The search for generality in studies of disturbance and ecosystem dynamics. – In: Esser, K. et al. (eds), *Progress in botany*. Springer, pp. 399–450.
- Wootton, J. T. 1994. The nature and consequences of indirect effects in ecological communities. – *Annu. Rev. Ecol. Syst.* 25: 443–466.