

Forum

Bringing the Eltonian niche into functional diversity

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Studies of functional diversity (FD) have gained immense interest because they promise a more mechanistic understanding of the relationship between diversity and ecosystem functioning. However, the concept of FD is currently not used to its full potential because of several biases and shortcomings. For instance, while the analysis of traits related to species' Grinnellian niches, i.e. traits influencing species' fitness under different environmental conditions, is well-advanced, there is a lack of studies on the functional diversity related to species' Eltonian niches, i.e. species' functional roles in ecological processes and their effects on other species, a discrepancy known as the *Eltonian Shortfall*. Most importantly, the current indirect approach of measuring FD via species traits restricts analyses to species with similar traits, usually a taxon. Consequently, FD is generally measured for only one taxon but across different ecological processes, when it would ideally be measured for one ecological process but across all taxa that contribute to that process. These discrepancies hinder advances of our understanding of the relationship between diversity and ecosystem functions and services. We introduce a new approach to measuring functional diversity that is designed to overcome these shortcomings by bridging research on networks, species niches, and functional traits. Instead of characterizing functional roles *indirectly* via species' traits, we propose to characterize functional roles *directly* via the traits of species' resources and interaction partners in a given ecological process. Critically, this shift in perspective for the first time allows comparisons of the functional roles of all taxa that participate in an ecological process regardless of their own morphology. We illustrate our new approach with a study on functional roles of frugivores in seed-dispersal systems. Our approach is an important addition to existing approaches to studying FD, and it facilitates new studies in a vastly unexplored field of functional diversity research.

Keywords: beta-diversity, ecological processes, ecosystem functioning, functional roles, Grinnellian niche, interaction networks, morphology, specialization, traits

Synthesis

We introduce an approach to measuring functional diversity that characterizes species' functional roles directly via their interactions and resource use. This facilitates studies of functional roles in processes related to species' Eltonian niches (but it can also be used to describe Grinnellian niches). Crucially, it allows the consideration of all taxa that participate in a given process regardless of differences in their morphology, which will advance our understanding of the relationship between diversity and ecosystem functioning. Our approach opens the door to comparative studies on species roles and functional diversity, convergent evolution, species invasions, and community assembly across spatial scales.



Introduction

Functional diversity (FD) aims to describe the diversity in species traits relevant for ecosystem functioning (Tilman 1999). FD is commonly measured as the diversity of trait combinations that reflect differences in species' adaptations to the environment and in their effects on other species, i.e. their functional roles (Tilman 2001, Petchey and Gaston 2002, Dehling et al. 2016). FD is increasingly preferred over classic diversity measures for species assemblages – such as species richness or species diversity – because it is regarded as a strong indicator for the resilience of ecosystems (Hughes et al. 2005) and was found to be more sensitive to ecosystem alterations and disturbances (Mouillot et al. 2013). It is therefore considered an important tool, for example, when assessing the effect of biodiversity loss on ecosystem functioning (Naeem et al. 2012).

Despite its potential usefulness, the concept of functional diversity is currently not used to its full potential because of a number of conceptual shortcomings and biases, as well as methodological limitations inherent to current approaches. For example, the study of the Grinnellian aspect of species niches (i.e. adaptations to environmental conditions) has received much attention in functional diversity research, and the field of trait–environment relationships is well-advanced, especially for plants (Wright et al. 2004, Blaum et al. 2011, Kattge et al. 2011, Reich 2014, Salguero-Gómez et al. 2015, Díaz et al. 2016). In contrast, the Eltonian aspect (i.e. direct interactions between species and their effects on each other) has been largely ignored (Rosado et al. 2016), mostly because of limitations in the availability of data and methods. Consideration of species' Eltonian niches, however, is crucial for understanding many ecological processes and, ultimately, the relationship between diversity and ecosystem functioning. Related to that, it is important to measure FD with respect to specific ecological processes that underlie the functions and services of interest, and to select traits accordingly (Cornelissen et al. 2003, Pérez-Harguindeguy et al. 2013, Dehling et al. 2014b, 2016). In practice, however, there is a recent tendency to measure FD as a general diversity of traits, i.e. without a definition of the ecological process of interest and without testing whether the selected traits are relevant for this specific process (Rosado et al. 2013, 2016, Mlambo 2014). Finally, and perhaps most importantly, the current practice of measuring FD indirectly via species traits restricts analyses to species with comparable sets of traits. As a result, FD is usually measured for a specific taxon, thereby explicitly ignoring the many species from other taxa that fulfil similar and/or complementary roles in the same ecological process. These shortcomings hinder advances of our understanding of the relationship between diversity and ecosystem functions and services. In the following, we elaborate on these problems regarding the current use of FD. We then present a new approach to measuring FD based on the Eltonian niche of species that is designed to overcome the problems.

The Eltonian shortfall

Related to the notion of function as “adaptation” (Bradshaw 1987), the widely-used definition by Violle et al. (2007) describes functional traits as “any morphological, physiological or phenological feature [...] which impact[s] fitness indirectly via their effects on growth, reproduction, and survival”. It has been argued that this definition of “functional trait” is incomplete; even though it includes a distinction between “response traits” and “effect traits” (Violle et al. 2007, de Bello et al. 2010), these effect traits refer to the effect of species' performance on processes like biomass production, but not to species' functional roles and effects on other species in ecological processes governed by direct interactions (Rosado et al. 2016). (Please note that in this article we follow the increasingly common distinction between Eltonian and Grinnellian niches as referring to species interactions and environmental conditions, respectively. We would like to point out, however, that species interactions and environmental conditions are included in both Elton's (1927) and Grinnell's (1917) descriptions of the niche). Current research on functional diversity mostly focusses on the Grinnellian aspect on species niches (their adaptations to environmental conditions), and while some studies also include traits related to species' diet (Pavoine et al. 2009), data and studies on the Eltonian aspect of the niche, especially with respect species' functional roles in specific ecological processes, are still scarce (but see e.g. Dehling et al. 2014b, 2016). This lack of information has been recognized as the ‘Eltonian shortfall’ (Peterson et al. 2011). The consideration of interactions between species and their mutual effects (i.e. their functional roles) is, however, essential to understand ecological processes and the relationship between diversity and ecosystem functioning (Díaz and Cabido 1997, Petchey and Gaston 2006, Vandewalle et al. 2010, Dehling et al. 2016). The identification and measurement of traits that describe species roles and effects on other species hence constitutes one of the most important tasks in ecology (Rosado et al. 2016), and we need methods to incorporate such data on species' Eltonian niches into analyses of functional diversity.

FD is measured without defining the ecological process and without selecting relevant traits

In order to understand ecosystem functions and services, it is necessary to understand the underlying ecological processes and the functional roles of species in these processes. In a local species assemblage, the diversity of functional roles fulfilled by all species in all ecological processes is described by the entirety of their (realized) Eltonian niches (Fig. 1a). In turn, the Eltonian niche of an individual species encompasses all the different functional roles that this species fulfils in different ecological processes (Fig. 1b). Consequently, a species' functional role in one specific ecological process corresponds to the portion of its Eltonian niche that is relevant for this particular process (Fig. 1c). In the following, we refer to this

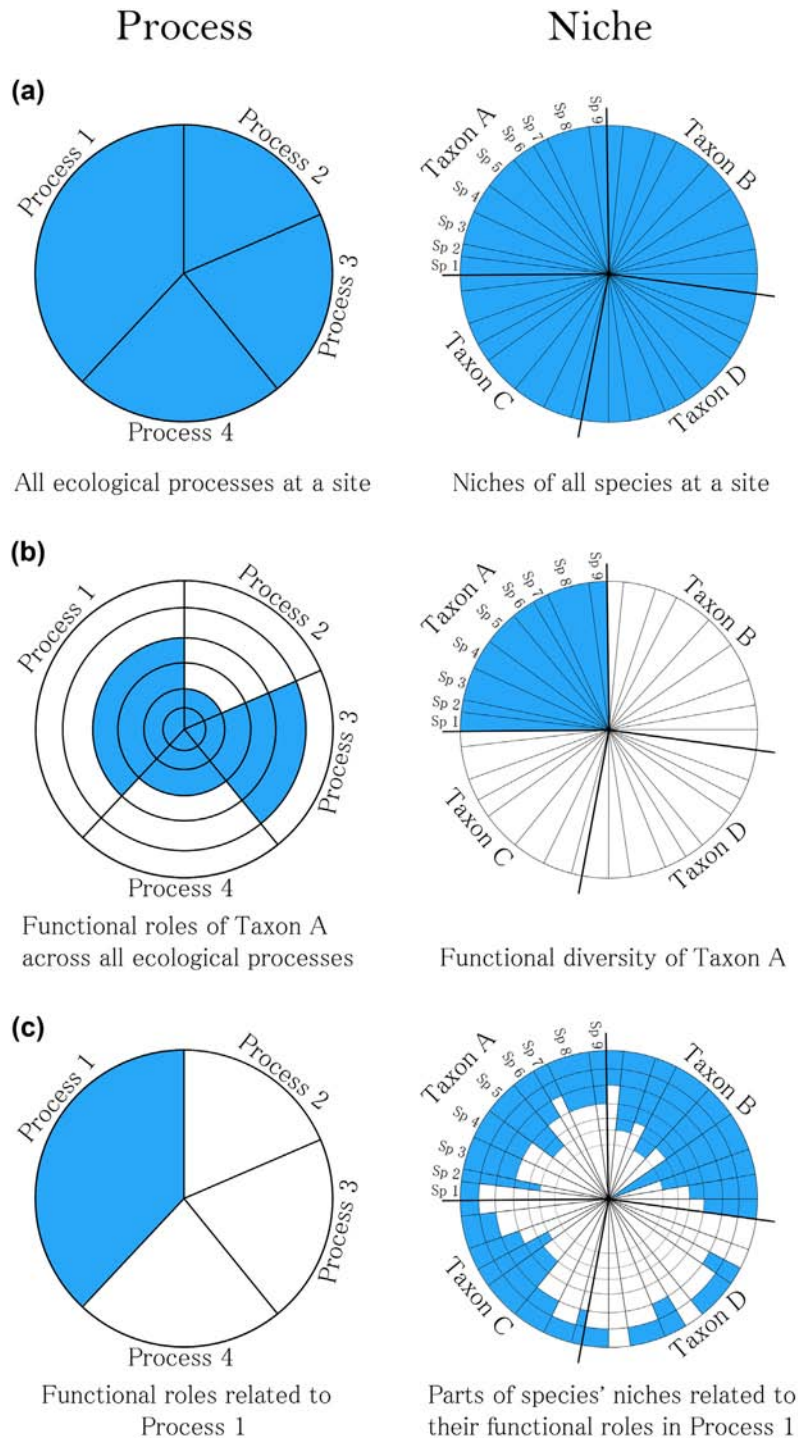


Figure 1. The relationship between ecological processes and species' niches. (a) At any given site, there are multiple ecological processes which are fulfilled by the local species assemblage. The niches of all species encompass species' functional roles in all of these ecological processes (i.e. their resource use and interactions with other species). The figure showcases four processes that are fulfilled by the species from four different taxa. The different sizes of the processes represent their local diversity, different sizes in niches represent differences in local abundance of the species. (b) Measuring functional diversity for a single specific taxon quantifies the functional roles of this taxon across different ecological processes but ignores functional roles fulfilled by species from other taxa. (c) The functional diversity of a species assemblage with respect to one particular ecological process is described by the cumulative process-related niches of all species that contribute to this process. The functional roles in this process are fulfilled by species from several taxa, and each species differs in the degree to which it contributes to this process. Note that the part of a species' niche that is relevant for one ecological process (the process-related niche, PRN) can also affect another process; for clarity, this is not shown here because the example is intended to highlight only the contribution to a single process.

portion of a species' Eltonian niche related to the species' role in a specific process as the process-related niche (PRN). The functional diversity of a species assemblage with respect to a particular ecological process is then described by the cumulative process-related niches of all species that contribute to this process (Fig. 1c).

The definition of functional traits as traits that influence a species' fitness (Violle et al. 2007) was criticised because this definition could arguably hold true for virtually every species trait, and, as a result, FD could be measured from a more or less arbitrary set of available traits that are at least minimally related to the natural history of a species (Mlambo 2014, Schmera et al. 2017). Likewise, Rosado et al. (2013) criticised the use of "fashionable traits" that are readily available for analyses on large spatial scales but whose effects are rarely analytically tested locally. Without a definition of the ecological process of interest, it is unclear what is being measured as "functional diversity", because functional traits can be related to different ecological processes (Fig. 1b), and different sets of functional traits are relevant for a species' roles in each ecological process (Dehling et al. 2014b, 2016). Calculating FD from loosely-defined functional traits could then either result in spurious differences between species assemblages driven by traits that are functionally irrelevant for the research question, or add noise and blur the differences in functionally relevant traits. In addition, the use of different sets of traits in different studies makes comparisons of functional diversity across studies, e.g. in meta-analyses, difficult or impossible. From early on, it was therefore advised that the selection of traits for analyses of functional diversity should be based on their relevance for specific ecological processes (Cornelissen et al. 2003), but studies that use quantitative tests to select traits for analyses of FD are still rare (but see Dehling et al. 2014b, 2016). While it should be self-explanatory (and most studies probably do a good job at selecting relevant traits), it is necessary to remind us that in order to understand the relationship between functional diversity and specific ecosystem functions and services, it is indispensable to 1) specify the ecological function or service of interest to the study, 2) identify the ecological processes underlying these functions and services, and 3) disentangle the functional roles of species in the different ecological processes.

FD is measured for a taxon when it should be measured for an ecological process

A particularly severe problem with the current way of measuring FD indirectly via trait adaptations is that this approach limits analyses of FD to species with similar comparable traits, usually a taxon. Functional roles in the same ecological process are, however, often fulfilled by species that are not closely related phylogenetically and therefore tend to have a completely different morphology. For instance, insects, mammals, and birds (and other taxa) pollinate plants, but the current approach to measuring FD makes it impossible to compare the functional roles of species from such distinct taxonomic groups (Fig. 2). As a

result, functional diversity is usually measured for only one taxonomic group at a time but across different ecological processes (e.g. 'the functional diversity of birds' or 'the functional diversity of mammals', Fig. 1b, 2b), when it would ideally be measured for a distinct ecological process (e.g. 'the functional diversity of pollinators' or 'the functional diversity of seed-dispersers', Fig. 1c, 2c). Restricting analyses of FD to a single taxon compromises the suitability of FD as a measure for the diversity of functional roles because an unknown number of roles fulfilled by other taxa is almost always ignored (Fig. 1). This especially affects comparisons of FD on large spatial scales, e.g. between regions or continents where similar functional roles in the same ecological processes are fulfilled by different taxa. We therefore need a way to study functional roles of species that allows the inclusion of all species that contribute to a particular ecological process.

A new approach to measuring functional diversity

We present a new approach to measuring functional diversity that complements existing approaches and that is designed to overcome the conceptual and methodological shortcomings outlined above. Instead of inferring a species' functional role indirectly from its possible trait adaptations to its resource use, we propose to assess the functional role directly by describing the species' resource use and its interactions with other species in a given ecological process. Conceptually, this definition of the functional role of a species is based around the idea of the Eltonian niche, which describes the role or "occupation" of species in a species assemblage (Elton 1927, Root 2001). These roles are best described by the traits of the interaction partners and resource species, for instance by the traits of the fruits that a seed-disperser disperses, the traits of the prey species that a predator consumes, or the traits of the flowers visited by a pollinator (Elton 1927, Dehling et al. 2016). Critically, shifting the focus away from the analysis of species' traits towards the analysis of the functional role itself via traits of resources and interaction partners 1) offers a way to analyse the functional roles of species and their effect on other species, 2) facilitates focusing the analyses on a particular ecological process, and, most importantly, it 3) allows the immediate inclusion of all species that contribute to an ecological process regardless of the idiosyncrasies of their own morphology (Fig. 2a–c). Our new approach of describing the diversity of species' functional roles complements existing methods to study FD, and it facilitates analyses in a neglected and therefore vastly unexplored field of functional diversity research. In addition, the shift in perspective facilitates several new ways of describing and comparing functional roles of species. For instance, we show how to measure the contribution of individual species to functional diversity and introduce it as a new measure for the functional specialization of species. We demonstrate the application of our new approach with data sets from seed-dispersal networks from the Peruvian Andes (Dehling et al. 2014b) and the Atlantic Forest in Brazil (Bello et al. 2017).

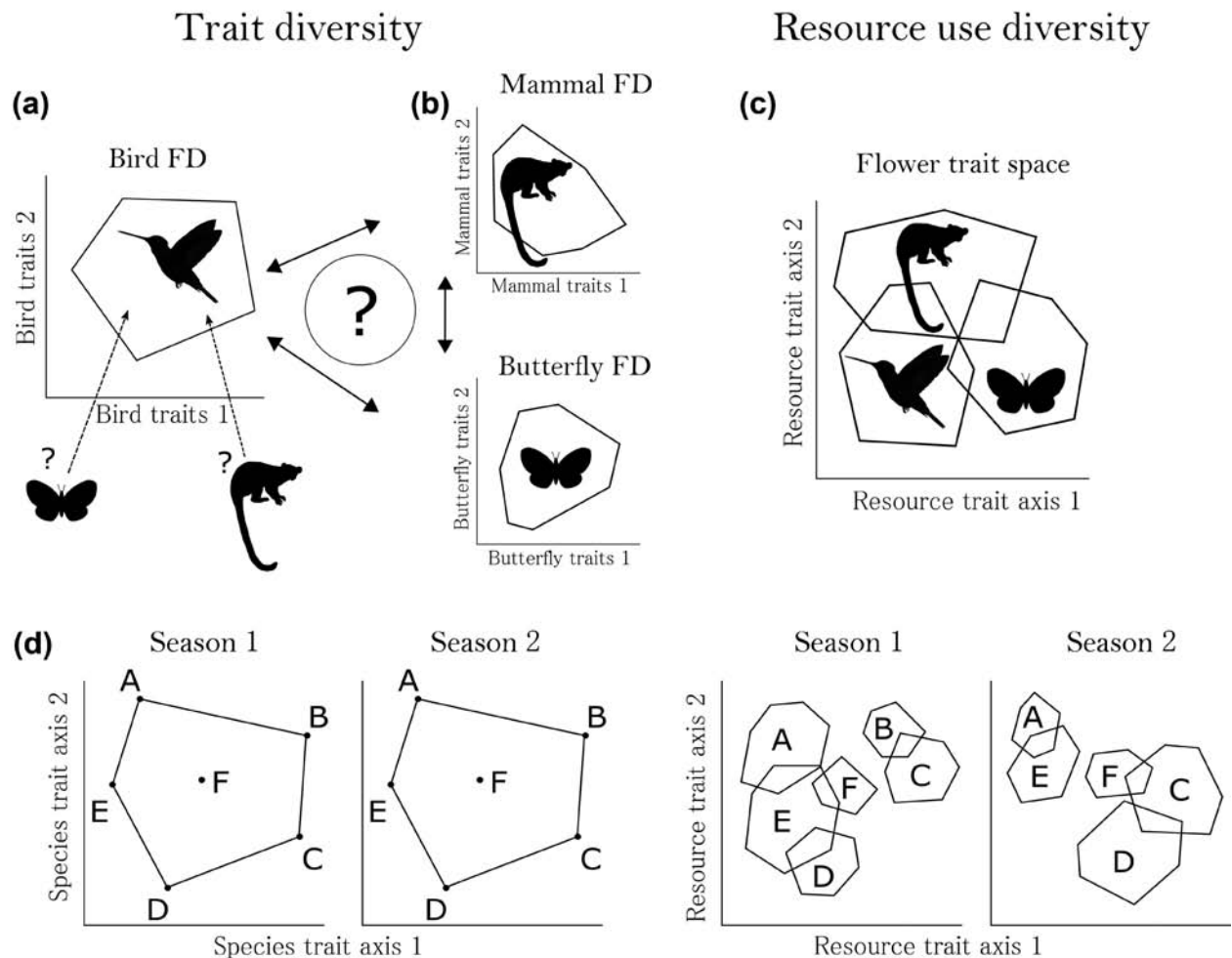


Figure 2. Analysing the diversity of functional roles across taxa, and across space and time. (a) Current approaches that measure FD as trait diversity can only consider species with the same sets of traits. Since different traits are usually relevant for describing functional roles in different taxa, it is impossible to compare the traits of different taxa (here exemplified for birds, mammals, and butterflies) in the same trait space. (b) As a result, FD is usually measured separately for the different taxa, but the relationship between the functional diversities of the different taxa is difficult to compare, which hinders a complete assessment of the functional roles within an ecological process. (c) Measuring functional diversity via species' resource use allows a comparison of functional roles of all taxa that participate in the same ecological process. (d) Measuring functional diversity from resource use facilitates taking into account seasonal and regional differences in functional roles of species. In the example, species composition of consumer species at a site is identical in two different seasons (left), but the species fulfil different roles, e.g. due to phenology or differences in the available resource species (right). For instance, note that in season 2, species B, although present at the site, does not fulfil any functional role in this particular ecological process, and, hence, does not contribute to the local FD. FD measured as trait diversity will give identical values, because the morphology of the consumer species remains the same (left), whereas calculating FD from consumer–resource interactions reveals these seasonal differences in functional roles (right).

To conclude, we provide an outlook on further applications of our approach.

Material and methods

Methodologically, our approach builds upon and extends the framework introduced by Dehling et al. (2016) who related the morphology of species to species' foraging preferences. We show here how this framework can be extended to measure and compare functional roles of species in an ecological process via their process-related niches. R code for all functions

is available on DMD's GitHub site (<<https://github.com/matthiasdehling>>).

Data on species interactions

Data on interaction partners and resource use will ideally come from highly resolved interaction networks. While the sampling of species interactions is time and cost intensive, the growing field of ecological network research already provides many highly resolved datasets on species interactions in local communities (e.g. Web of Life, <www.web-of-life.es>), some of which even include seasonal repetitions (Dehling et al.

2014b, Saavedra et al. 2016). Many more such datasets will become available in the future. Alternatively, data on resource use and interaction partners can be compiled from published sources, such as monographs or handbooks. In addition, newly developed methods such as isotope analysis and metabarcoding (Jackson et al. 2011, Layman et al. 2012) are promising approaches that might facilitate the inference of species interactions for a large number of species in local communities in a less labour-intensive fashion in the future.

The process-related niche of a species

The process-related niche (PRN) of a species is described by the diversity of the trait combinations of a species' interaction partners or resources in the context of an ecological process (for simplicity hereafter called 'resources'). As is common

with existing approaches to analysing FD (Mason et al. 2005, Villéger et al. 2008, Schmera et al. 2017), we analyse resource traits in a multidimensional trait space. With principal coordinates analysis, we first project resource species into a multidimensional space, where they are arranged according to their relative trait values (Fig. 3a–c). The selection of functional traits that characterize resource species and build up the trait space is important as it will influence all analyses. It should therefore be based on a careful identification of the traits that are functionally relevant for the ecological process that is studied (Mlambo 2014, Dehling et al. 2016, Schmera et al. 2017), and traits should ideally be selected based on quantitative tests (Dehling et al. 2014b). The PRN of a species is then given by the convex hull in the projected multidimensional space that includes all resource species with which the species interacts (Fig. 3a–c).

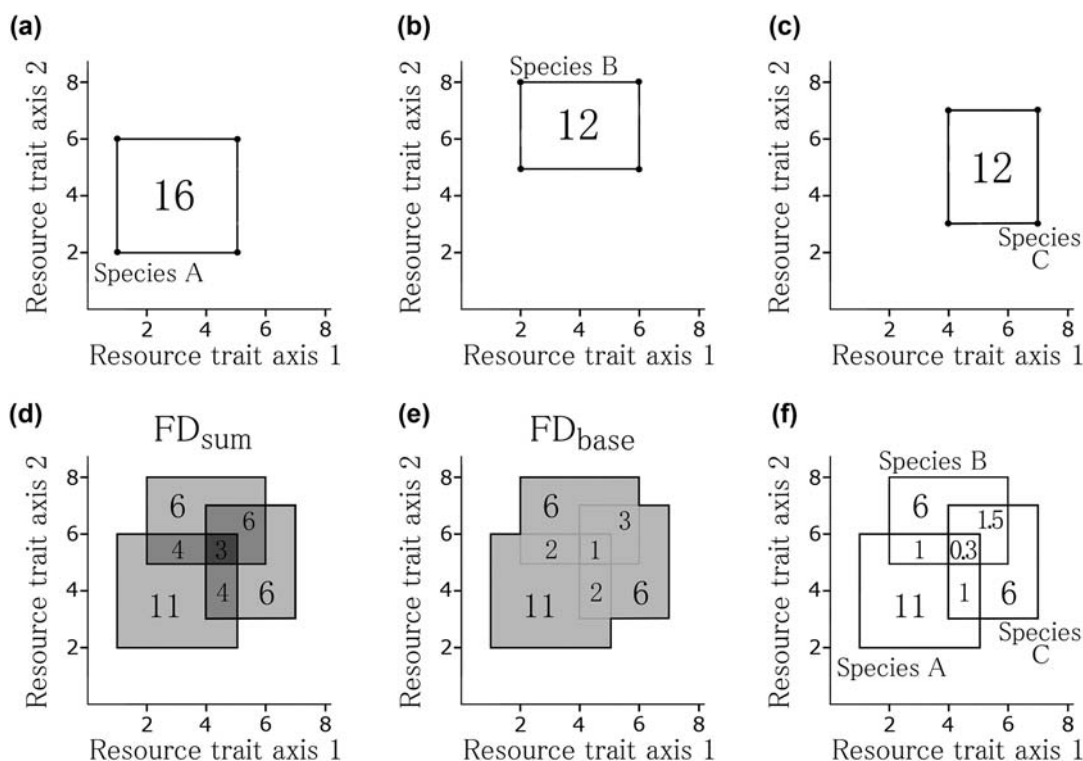


Figure 3. Process-related niches, functional diversity, and individual contribution to FD. The process-related niche, PRN, describes the functional role of a species in a given ecological process. It constitutes the part of a species' niche that is relevant for that particular process, characterized by the traits of the resources and interactions partners of the species. (a–c) For each consumer species, the PRN is quantified as the convex hull that includes the points of all resource species projected into a multidimensional trait space, shown here as open squares. The functional diversity of a species assemblage can be described in two ways: (d) FD_{sum} is calculated as the sum of the individual volumes of the PRNs of all species, regardless of whether or not they overlap. In the example, FD_{sum} is 40. (e) FD_{base} describes the range of resources used by all species of a species assemblage, and hence the range of functional roles fulfilled by the species of an assemblage, ignoring the overlap in the PRNs. In our example FD_{base} is 31. The ratio between FD_{sum} and FD_{base} provides an estimate of the redundancy of the functional roles of species in an assemblage. (f) The contribution of a species to FD_{base} is calculated as the weighted PRN: each part of a species' PRN that it shares with n other species is divided by $n + 1$ (species A: 13.33, species B: 8.83, species C: 8.83). The weighted PRNs of all species sum up to the FD_{base} of the assemblage. The relative individual contribution of a species to FD_{base} is the ratio between its weighted PRN and FD_{base} (species A: 0.43, species B: 0.285, species C: 0.285). The contribution of each individual species to FD_{sum} is the volume of its PRN (a–c). The relative contribution of each species to FD_{sum} is the ratio between the volume of a species' PRN and FD_{sum} (species A: 0.4, species B: 0.3, species C: 0.3). Finally, the unique contribution of a species to FD is the part of its PRN that is not shared with any other species (species A: 11, species B: 6, species C: 6). Together, these measures provide an indication of the possible importance or redundancy of species for the ecological process.

Please note that the greatest novelty of our approach lies in the shift in perspective away from analysing species own trait adaptations towards analysing the traits of species' resources and interaction partners. We exemplify it here by analysing trait combinations in a multidimensional trait space analogous to the convex hull approach by Villéger et al. (2008, 2011). While the advantages and disadvantages of convex hulls are debated (Blonder 2016, Carmona et al. 2016a, b), we chose to use them because they are a very intuitive representation of the niche, and therefore excellently suited to illustrate our approach. We want to remark, however, that the quantification of the process-related niches via the traits of a species' resources and interaction partners can also be performed using other methods (Blonder et al. 2014, Carmona et al. 2016a).

The functional diversity of species assemblages

We propose two measures to quantify the functional diversity of a species assemblage given the set of relevant PRNs. The first measure, FD_{sum} , is calculated as the sum of the individual volumes of the PRNs of all species (Fig. 3d). The second measure, FD_{base} , describes the range of functional roles – the cumulative PRN – of a species assemblage (Fig. 3e). It is measured as the functional richness of all resources, measured as the total volume of the union of the PRNs of all consumer species. FD_{base} hence ignores the possible overlap in species' PRNs, and regions in trait space that are covered by more than one consumer species are counted only once (Fig. 3e). In contrast, FD_{sum} is influenced by both the full range of functional roles as well as the density with which these roles are covered. This implies that FD_{sum} can be examined in relation to FD_{base} to provide an estimate of the redundancy of species' functional roles. If species hardly overlap in their PRNs, FD_{sum} is similar to FD_{base} , and the redundancy is small; if PRNs overlap widely, FD_{sum} is much bigger than FD_{base} , and the redundancy in functional roles is high. Note that both FD_{base} and FD_{sum} can be applied at any spatial scale because they are calculated based on the range of resources used, either from individual PRNs or cumulative PRNs. Hence, they can be measured as the diversity of trait combinations of the resources and interaction partners of individuals, species, species assemblages or even species pools of entire biogeographic regions. The convex hull of the PRN only considers the presence but not the frequency with which a resource is used, i.e. it does not take into account differences in species' preferences for certain parts of their PRNs. The analysis of FD can therefore be combined with an analysis of species' foraging preferences (the centroids of species' PRNs, calculated as the mean coordinates of each species' resources, weighted by the frequencies with which the resources are used, see Dehling et al. 2016 for details).

Functional specialization and the contribution of individual species to functional diversity

Functional specialization describes the degree to which a species' functional role differs from those of other species. This depends both on the size and the position of a species' niche

relative to those of other species. The existing approaches of calculating FD from trait adaptations can only calculate specialization based on differences in species' niche position, approximated by the position of a species' trait combination in multidimensional trait space (Bellwood et al. 2006, Schmera et al. 2009), either as uniqueness – the distance to the species with the most similar trait combination – or originality – the distance between a species' trait combination and the average trait combination of the assemblage (Bellwood et al. 2006, Buisson et al. 2013). This does not reflect the overlap in the range of resources used by species, and hence the potential redundancy or complementarity in species' contribution to an ecological process. In contrast, our new approach of calculating functional diversity from species' niches offers a way to determine the specialization of a species' functional roles taking into account both species' niche sizes and niche positions via the relative overlap of a species' PRN with that of other species. PRN overlap provides a measure of the exclusiveness of species' resource use and facilitates the quantification of the contribution of each individual species to the overall functional diversity of a species assemblage.

The individual contribution of a species to FD_{sum} is given by the volume of its PRN. The relative contribution can then be expressed as the ratio between the volume of the PRN and the volume of FD_{sum} . The contribution of species to FD_{sum} is therefore only influenced by the size of their niches. Calculating the individual contribution to FD_{base} is slightly different because it also takes into account the overlap of a species' PRN with the PRNs of different species. The contribution of a species to FD_{base} is therefore calculated as the weighted PRN (Fig. 3f). For each consumer species, we determine which part of its PRN overlaps with those of other species. We then divide the volume of each part of the PRN by the number of species that overlap in that part; that is, the part of a species' PRN that it shares with n other species is divided by $n + 1$ (Fig. 3f). The weighted PRNs of all species sum up to the FD_{base} of the assemblage, and the relative contribution of a species to FD_{base} is calculated as the ratio between weighted PRN and FD_{base} . Note that the weighted PRN can also be used to identify species with a unique contribution to FD – i.e. species whose PRNs do not or only partly overlap with those of other species (Fig. 3f). Together with the individual contribution, this can serve as another measure for the contribution of a species to the ecological process and, hence, the possible importance of a species. In addition, analyses of individual contribution to FD can be combined with measures of the specialization of species' foraging preferences (Dehling et al. 2016) to take into account differences in species' preferences for certain parts of their PRNs.

Functional beta diversity

Functional beta diversity describes differences in the diversity and composition of functional roles between two species assemblages (Villéger et al. 2011). In our approach, it is measured as the differences in the positions in trait space of the PRNs of the species from two species assemblages, either calculated as βFD_{base} or as βFD_{sum} (Fig. 4). βFD_{base} assesses

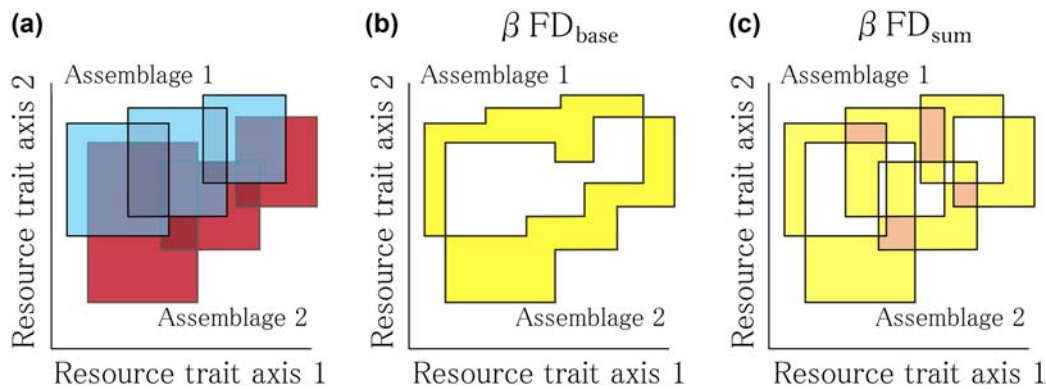


Figure 4. Functional beta diversity. (a) Functional beta diversity is the change in the diversity and composition of functional roles between two assemblages, measured as difference in the coverage of trait space by species' PRNs. (b) βFD_{base} assesses the change in the coverage of trait space between two species assemblages. Regions covered by both assemblages are shown in white, regions covered by only one species assemblage are shown in yellow. βFD_{base} thus provides an estimate of whether any roles are lost or gained between assemblages. (c) βFD_{sum} assesses the change in the density of PRNs in different parts of the resource trait space between two assemblages. In the example, white areas symbolize no change, yellow areas changes of $|1|$, orange changes of $|2|$. βFD_{sum} provides an estimate of whether functional roles are fulfilled by a different number of species in two assemblages.

the changes in coverage of trait space by the PRNs of two species assemblages. It provides an estimate of whether any roles are lost or gained between two assemblages (Fig. 4b). βFD_{sum} assesses the change in the density of PRNs in different parts of the resource trait space between two assemblages. This provides an additional estimate of whether functional roles are fulfilled by a different number of species in two species assemblages (Fig. 4c). Both measures of βFD are calculated directly from the coverage of trait space by the two species assemblages and can easily be partitioned into the regions of trait space covered by either of two assemblages and the regions shared by two assemblages, as well as the densities with which these regions are covered. It is therefore possible to use any index for beta diversity to quantify βFD as changes in coverage (βFD_{base}) and changes in density (βFD_{sum}) analogous to measuring changes in species composition as differences in species' presence/absence or changes in species abundances, respectively. In addition, this allows dividing βFD into its nestedness and turnover components (Baselga 2010, Soininen et al. 2018) which makes it straightforward to quantify the functional roles gained, maintained or lost between two species assemblages. In the examples below, we quantify βFD as the total change in the coverage of the trait space between two assemblages. In this case, βFD is bound between 0 (if the assemblages cover the same regions of trait space with the same density) and the sum of the individual FD values (if the assemblages do not overlap at all in their resource use). βFD can be standardised by this maximum value so that values fall between 0 and 1.

Case study: functional roles of frugivores in seed-dispersal systems

We illustrate our new approach to measuring functional diversity by analysing the functional roles of frugivorous birds in the tropical Andes of Peru (Dehling et al. 2014b). This data set consists of two extensively sampled local interaction

networks (Wayqecha, 3000 m a.s.l., 13°2S, 71°6W; San Pedro, 1500 m a.s.l., 13°1S, 71°6W; details in Dehling et al. 2014b), and we illustrate the calculation of FD_{base} , FD_{sum} , βFD_{base} , βFD_{sum} , and individual contribution of species to FD. In addition, we analyse functional roles in a network sampled across four different taxa of frugivores (birds, mammals, reptiles and fish) in the Brazilian Atlantic Forest (Bello et al. 2017) to illustrate differences in the contribution of different taxa to functional diversity. For the Peruvian networks, we determined resource use of co-occurring bird species (26 species in Wayqecha, 61 species in San Pedro) based on four plant traits that have been identified in quantitative tests to be functionally relevant for foraging choices of frugivores (fruit length, fruit diameter, plant height, crop mass; Dehling et al. 2014b). For the Brazilian network, we determined resource use of 281 frugivore species (208 birds, 81 mammals, 5 fishes and 2 reptiles) based on fruit length, fruit diameter, seed length and seed diameter (Bello et al. 2017). For each data set, we projected plant species into a four-dimensional trait space. For each consumer species from each network, we then calculated the process-related niche (PRN), and from these, we calculated FD_{base} and FD_{sum} from the PRNs for each site. We determined individual contribution of each species to local FD_{base} and FD_{sum} . For the Peruvian networks, we also calculated βFD_{base} and βFD_{sum} between the two sites.

Results Peru

FD_{base} and FD_{sum} were larger in San Pedro (5873 and 19 590, respectively) than in Wayqecha (3736 and 8973, respectively). Functional roles in the San Pedro network were covered by relatively more species (ratio $FD_{sum} / FD_{base} = 3.33$) than in Wayqecha (ratio $FD_{sum} / FD_{base} = 2.40$). βFD_{base} between the sites was 6447, βFD_{sum} was 21 911, or 0.70 and 0.77, respectively, compared with the maximum possible value. Most

of the beta diversity can be attributed to size differences in the functional trait spaces between the sites indicating that a large number of functional roles are not realized in the assemblage at the higher elevation (Dehling et al. 2014a, b). In Wayqecha, individual contributions of species to FD_{sum} varied from 0.08% in the flowerpiercer *Diglossa sittooides* to 24.6% in the mountain-tanager *Buthraupis montana*. Individual contribution of species to FD_{base} varied from 0.09% in the tanager *Tangara nigroviridis* to 25.5% in the mountain-toucan *Andigena hypoglauca*. Species with low contribution to FD are opportunistic frugivores that are also relatively rare at the sites whereas species with the highest contribution to FD are obligate frugivores. In San Pedro, individual contribution of species to FD_{sum} and FD_{base} was lowest in the parakeet *Aratinga leucophthalmus* (0.08% and 0.02%, respectively) and highest in the Andean Cock-of-the-rock *Rupicola peruvianus* (17.7% and 35.9%, respectively). *Aratinga leucophthalmus* is rare at the site, *Rupicola peruvianus* is a common, though not abundant, obligate frugivore at the site.

Results Brazil

FD_{base} in the Brazilian network was 28 744, FD_{sum} was 156 538. Birds, mammals, fish and reptiles contributed 48.0, 51.8, 0.2 and 0.1 percent to FD_{base} and 64.3, 35.0, 0.4 and 0.2 percent to FD_{sum} , respectively. The high percentages of FD_{base} and FD_{sum} contributed by either the main frugivore groups, birds and mammals, show that a large percentage of the diversity of functional roles would be lost if only one of the taxa were studied.

Discussion

We have introduced here a new conceptual approach to measuring functional diversity. The new approach differs from previous ones in that we characterize functional roles of species directly based on species' niches instead of characterizing functional roles indirectly via trait adaptations. Conceptually, this has two major implications. First, by characterizing the functional role of a species by its resource use and interaction partners, our approach offers a way to take into account the Eltonian aspect of a species' niche; that is, the functional roles of species that are related to their direct interactions with and effects on other species. Our approach hence represents a major step in functional-diversity research towards overcoming what has been described as the 'Eltonian shortfall', the lack of information regarding species' functional roles and effects (Peterson et al. 2011). Secondly, our approach is also the first to provide a methodological framework that facilitates comparisons of functional roles and functional diversity across taxa, independent of their own morphology, which allows comparisons of FD between sites and regions where similar functional roles are fulfilled by different taxa. Our approach hence represents a shift away from quantifying

FD for a specific taxon across different ecological processes towards quantifying the diversity of functional roles for a specific ecological process across all species that contribute to these processes. As shown by our analysis of the functional roles in the Brazilian seed-dispersal system, different taxa – while overlapping partly in their functional roles – contributed rather differently to ecological processes. Restricting analyses to only one taxon hence ignores a large part of the diversity of functional roles fulfilled by other taxa in the same ecological process. Our new approach complements existing approaches to studying FD, and while in some circumstances it will remain advantageous and desirable to study trait variation in a single taxon (e.g. when studying trait evolution or for taxa that serve as biological indicators), it opens up avenues for new questions and analyses in a largely unexplored field of functional diversity research. The study of functional roles in ecological processes related to the Eltonian niches of species will advance our understanding of the relationship between functional diversity and ecosystem functioning, as well as of the mechanisms governing ecological communities.

Our approach also overcomes several methodological limitations inherent to approaches to measuring FD indirectly via trait adaptations. For instance, the functional role of a species in an ecological process might change in space and time because the set of available resources differs between sites or between seasons (Bender et al. 2017), because a consumer species only seasonally participates in a particular ecological process, or because its functional role might differ between sites depending on the presence of other species with overlapping functional roles (Fig. 2d). When measuring functional diversity from trait adaptations, each species is only represented by a single point that represents the average morphology of that species (Petchey and Gaston 2002, Mason et al. 2005, Villéger et al. 2008, but see Carmona et al. 2016a). While it has been shown that the morphology of a species can reflect its average niche position or average foraging preference (Dehling et al. 2016), the morphology of a species does not change temporally or locally to the extent that it reflects the change in the species' resource use, and therefore it cannot reflect the temporal or local differences in its functional roles (Fig. 2d). In contrast, calculating FD directly from the process-related niches makes it straightforward to account for local and temporal differences in functional roles, because the PRNs, and thus FD, can be calculated for different spatial and temporal scales, based on the set of resources exploited by the species at the respective point in time and space (Fig. 2d).

For similar reasons, it has not been possible to date to quantify the contribution of individual species to functional diversity. As before, the distance between species in trait space (i.e. the similarity between their mean trait combinations) reflects the similarity in their average foraging preferences or niche positions (Dehling et al. 2016). Accordingly, a species' contribution could only be approximated by measuring the distinctiveness of a species' niche position (Dehling et al. 2016), often approximated by the species' morphology, for example as uniqueness – the distance to the species with the

most similar trait combination – and originality – the distance between a species' trait combination and the average trait combination of the assemblage (Bellwood et al. 2006, Buisson et al. 2013, Blonder et al. 2014, Carmona et al. 2016a, Violle et al. 2017) or as the mean distance to all other species in an assemblage (Sasaki et al. 2009, Schmera et al. 2009). These measures provide an idea about differences in species' niche positions, but not about differences in the size and overlap of species' niches, and hence the potential redundancy or complementarity in species' contribution to an ecological process. In contrast, our approach makes it straightforward to quantify the individual contribution of species based on the overlap in their PRNs. Our examples from the Peruvian data set showed that species can differ enormously in their individual contributions to ecological processes with many species contributing little, and few species fulfilling the vast majority of functional roles. Our approach facilitates new studies on spatial and temporal differences in species' functional roles in and individual contribution to ecological processes, which will help to gain insight into the mechanisms governing these processes as well as the structure of species assemblages.

Although one major aim of our study was the development of a way to include the Eltonian aspect of species' niches into analyses of functional diversity, our approach is not limited to describing only the functional roles of species and their effects on other organisms (the Eltonian aspect of the niche) but it can also be used to describe the requirements of a species (the Grinnellian aspect of the niche, i.e. the range of combinations of environmental conditions), both within the same framework (Fig. 5). For instance, instead of using species traits that indirectly and imperfectly describe species' adaptations to environmental conditions, one could use the range of environmental conditions directly (Parravicini et al. 2015), which could be an advantage, especially in cases where an adaptation to an environmental condition is not manifested in traits. In fact, despite calling it a change in perspective, our approach of describing the requirements and functional roles of species directly rather than by trait adaptations is in accordance with Elton's original definition of the niche: namely, a description of "what an animal does, not what it looks like" (Elton 1927), and this is equally true for both the Grinnellian and the Eltonian aspect of the niche.

Likewise, we wish to avoid giving the false impression that our approach is only suited to describe the functional roles of animals with respect to their Eltonian niche. In actuality, it is equally suited to describe the functional roles of plants or any other organism with regard to their roles as interaction partners and their effect on other species, and we hope that this will facilitate analyses in understudied groups such as microbes for which measuring the diversity of roles is particularly needed. Moreover, while the knowledge about functional traits is arguably better in plants than in animals (Blaum et al. 2011, Wright et al. 2004, Kattge et al. 2011, Reich 2014, Salguero-Gómez et al. 2015), it could – depending on the question and type of analysis – sometimes be more straightforward to use

variables that describe species' requirements directly instead of first having to identify traits that (imperfectly) describe the adaptations to these requirements, especially in cases where these relationships are not known and even unlikely to be found. Our approach would then offer a way to describe plant functional diversity not by the diversity of trait adaptations that represent plant responses and effects alone, but also by the responses and effects themselves. It therefore offers a complementary way to study trait–environment–fitness relationships. Describing the functional roles of species and their effect on other species via resource use and species interactions opens the door to describing other roles of plants, beyond the production of biomass. While the study of FD is outlined to answer two main questions, namely 1) how species influence the ecosystem, and 2) how species correspond to changes in the environment (Hooper et al. 2002), so far, descriptions of the spectrum of forms and functions in plants (Díaz et al. 2016) focus on descriptions of the latter, i.e. the adaptations of plants to different environmental conditions. This does not take into account the diversity of effects that plants have on other organisms, for instance as interaction partners in mutualistic relationships, as habitat, or even for ecosystem services, e.g. related to tourism (Grünwald et al. 2016, Arbieu et al. 2017) or human well-being (Lindemann-Matthies et al. 2010, Bakolis et al. 2018). The framework introduced in this article offers a methodological base for these new kinds of analyses that complement the existing – already very advanced – fields of FD research.

Outlook

Further applications of the framework: using niches to improve studies on species assembly

Apart from characterizing species' functional roles, our approach can also be used for different analyses that are closely related to analyses of FD. For instance, the increasingly popular studies of community assembly and assemblage structure are commonly based on the comparison of species' trait adaptations in multidimensional trait spaces or approximations thereof based on phylogenetic relatedness (Webb et al. 2002, Bryant et al. 2008, Cavender-Bares et al. 2009, Graham et al. 2009, Dehling et al. 2014a). These analyses compare pairwise trait or phylogenetic differences of species from an empirical species assemblage against values obtained under random species assembly (Webb et al. 2002). Differences in the amount and regularity of the distribution of species in trait space are then used to infer mechanisms underlying assemblage structure. Larger-than-random mean pairwise distances between species are often attributed to competition based on the assumption that species with similar trait adaptations cannot coexist, whereas smaller-than-random pairwise distances are attributed to environmental filtering based on the assumption that at some sites occurrence is limited to species with certain, non-random trait combinations (Cavender-Bares et al. 2009, Graham et al. 2009). Early on, this interpretation was criticised as being too simple

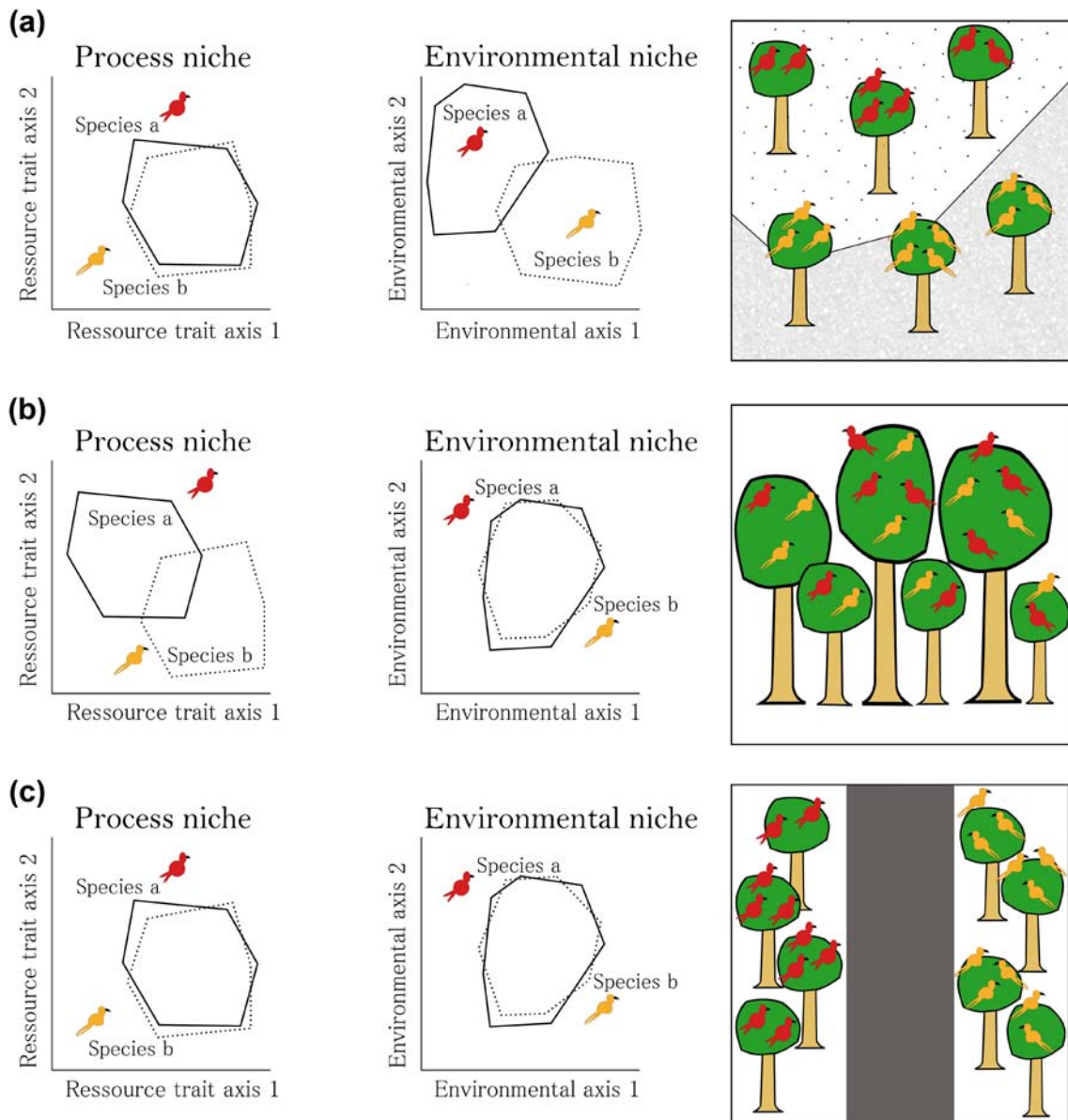


Figure 5. Process niche and environmental niche. Different combinations of resource use (process niche or ‘Eltonian niche’) and environmental requirements (environmental niche or ‘Grinnellian niche’) in two species. (a) Species might use similar resources and, hence, fulfil a similar functional role in the species assemblages to which they belong. However, since they differ in the environmental conditions under which they can occur, they replace each other in species assemblages along environmental gradients, e.g. in different habitats. (b) In contrast, two species might use different resources but have similar environmental requirements. They can co-occur in a local species assemblage because they fulfil different functional roles. (c) Finally, two species might have almost identical functional roles and environmental requirements, but they occur in species assemblages that are separated by a significant barrier, e.g. a large river, an ocean or a mountain chain. If one species eventually crosses the barrier, it might either fail to establish itself due to the high niche overlap with the other species, or it might outcompete the resident species and eventually replace it (e.g. in the case of invasive species). Knowledge and consideration of both resource use (‘Eltonian niche’) and required environmental conditions (‘Grinnellian niche’) are needed for understanding the current distribution of species and simulating their potential distributions in the future.

(Mayfield and Levine 2010, HilleRisLambers et al. 2012, Dehling et al. 2014a) because it ignores the fact that different traits reflect the resource use (and hence potential competition) versus the adaptation to environmental conditions (which can also be relevant for competition). Some studies have tried to overcome these limitations by studying a specific

foraging guild that uses the same resources (Dehling et al. 2014a) or different, single traits related to different aspects of community assembly (Trisos et al. 2014). Nevertheless, the biggest shortcoming of these analyses is that they infer ecological differences between species from trait differences, and hence face the same limitations that we discussed for

the indirect approaches of quantifying functional diversity; that is, they 1) are restricted to a single taxon, 2) cannot take into account temporal and spatial differences, and 3) can only compare similarity of niche positions as opposed to the overlap in resource use. Comparing differences between species not based on species traits but on species' niches (i.e. resource use and environmental requirements) and the possibility to include all species that use the same resource – as introduced in this article – should help to better disentangle the influence of different abiotic and biotic factors, such as environmental filtering and competition, on the assembly of ecological communities.

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