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Review and Synthesis

Unifying functional trait approaches to understand the assemblage of ecological communities: synthesizing taxonomic divides

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Functional traits have long been considered the 'holy grail' in community ecology due to their potential to link phenotypic variation with ecological processes. Advancements across taxonomic disciplines continue to support functional ecology's objective to approach generality in community assembly. However, a divergence of definitions, aims and methods across taxa has created discord, limiting the field's predictive capacity. Here, we provide a guide to support functional ecological comparisons across taxa. We describe advances in cross-taxa functional research, identify gaps in approaches, synthesize definitions and unify methodological considerations. When deciding which traits to compare, particularly response traits, we advocate selecting functionally analogous traits that relate to community assembly processes. Finally, we describe at what scale and for which questions functional comparisons across taxa are useful and when other approaches may be more constructive. Our approach promotes standardized methods for integrative research across taxa to identify broad trends in community assembly.

Keywords: community ecology, comparative ecology, cross-taxa comparison, functional ecology, functional traits

Introduction

A key challenge in community ecology is to identify drivers of species distributions and assembly. Throughout its history (Laureto et al. 2015), trait-based perspectives have advanced our understanding of major ecological processes, including niche differentiation (McGill et al. 2006, Blonder 2017), response to environmental disturbance (Flynn et al. 2009, Mouillot et al. 2013, Kimball et al. 2016, Fountain-Jones et al. 2017), and community assembly via environmental filtering (Lebrija-Trejos et al. 2010, Aronson et al. 2016). Identifying processes consistent with trait–environment relationships across co-occurring species and functional groups at a given spatio-temporal scale may promote the discovery of generality in

community ecology. For example, identifying traits common among ecological invaders, urban specialists or species resilient to climate change can help inform policy and management, as well as improve understanding of community assembly processes. Despite significant advances in the field, functional ecologists still seek to identify generalizable patterns between trait variation and environmental conditions, especially across taxa and scales (Jarzyna and Jetz 2018, Kissling et al. 2018).

Trait-based approaches, which attribute morphological differences to performance, fitness and ecological effects, provide a means of categorizing organismal variation in a standardized way while also accounting for the eco-evolutionary dynamics that shape communities. However, functional ecologists do not always explicitly relate traits to hypotheses and community assembly (see Discussion in Perronne et al. 2017, Brousseau et al. 2018), and often use divergent methods and definitions (as discussed by Vandewalle et al. 2010, Fountain-Jones et al. 2015, Perronne et al. 2017). Disagreement also exists on deciding which traits to measure, since different research questions or taxa often require distinct considerations in trait selection (see commentary in Poff et al. 2006 on considerations of trait-linkages and the discussion of trait selection in Pérez-Harguindeguy et al. 2013). Trait selection becomes especially significant when considering the sensitivity of different functional diversity measures to trait selection (Pakeman 2014).

A unification of functional trait approaches is needed to address discontinuity, improve standardization and allow for taxonomic comparisons (Vandewalle et al. 2010, Fountain-Jones et al. 2015, Moretti et al. 2017, Perronne et al. 2017, Degen et al. 2018, Schneider et al. 2018). Several studies have sought to better standardize trait selection within and across taxa, and many have found trait convergence with community assembly processes (Frenette-Dussault et al. 2013, Pedley and Dolman 2014, Brousseau et al. 2018). However, most of these studies compare taxa which have a strong history in functional ecology (i.e. plants). Still lacking is a synthesis of perspectives across a diversity of taxa that supports advancement towards generalizability and consistency in comparison of community assembly processes.

Here, we provide a guide for researchers conducting cross-taxa functional trait analyses to understand community assembly. We describe advancements in defining, collating and comparing morphological and physiological traits (i.e. response traits) across taxa, identify gaps in approaches that prevent successful cross-taxa comparisons and synthesize definitions and methodological considerations to better approach predictability in community assembly. We also identify when and in what contexts functional comparisons across taxa are most helpful and when other strategies may be more effective. Finally, we discuss how to apply these constructs to human-mediated traits and effect traits, as well as possible applications for future research.

Advancements and limitations in cross-taxa comparisons of functional traits

Advancements

Since the advent of functional ecology as a field (Calow 1987), several advances have strengthened collaboration across disciplines. In 2002, Lavorel and Garnier synthesized work by Keddy (1992), Chapin et al. (2000), and others to link traits that influence an individual's fitness and performance (i.e. response traits) with those that affect ecosystem function and/or an organism's environmental role (i.e. effect traits) (see Glossary). Subsequent work has enhanced the scope of functional ecology, including efforts to better classify plant functional types (Lavorel et al. 2007), predict vegetative responses to global change (Suding and Goldstein 2008), and link plant traits with ecosystem service provisioning (Lavorel and Grigulis 2012). Researchers have also compared trait distributions in three-dimensional niche space (McGill et al. 2006, Blonder 2017) and tested which functional traits best predict species distributions (Blonder 2017). Functional trait perspectives are also increasingly used to understand how biodiversity influences ecosystems under global change (Suding and Goldstein 2008, Tscharntke et al. 2008, Ahumada et al. 2011, Cardinale et al. 2012).

Many advancements have improved the standardization and collation of trait data. Handbooks and protocols exist for various taxa (e.g. plants (Cornelissen et al. 2003, Pérez-Harguindeguy et al. 2013), terrestrial invertebrates (Fountain-Jones et al. 2015, Moretti et al. 2017, Brousseau et al. 2018), benthic invertebrates (Degen et al. 2018), soil invertebrates (Pey et al. 2014), protists (Altermatt et al. 2015), lotic species (Schmera et al. 2015) and macrofungi (Dawson et al. 2019)). The creation of trait databases and datasets facilitates functional analyses across a diversity of taxa, including invertebrates, microbes, plants, birds, mammals, reptiles, amphibians, fungi and coral (see Schneider et al. 2018 Appendix Table A1 for a full list). To improve the uptake, scope and scale of trait-based research within and across taxa, there is a concerted effort to create global, multi-taxa trait databases (Schneider et al. 2018, the Open Traits Initiative (http://opentraits.org/)). These efforts support the use and accessibility of trait data, and their associated standards accelerate the growth of functional ecology.

Limitations

Cross-taxa comparisons are limited by variation in the measurement of selected traits across disciplines and the development of standards and resources for trait collation. Plants and invertebrates have widely accepted protocols for defining, collecting and analyzing functional traits, as well as trait databases. Other taxa, including mammals, reptiles and amphibians, lack standardized handbooks for protocols (Petchey and Gaston 2006, Vandewalle et al. 2010), and many broad groups of organisms (e.g. invertebrates) have

Glossary

Functional trait: Aspects of phenotypes (physiological, morphological or behavioral) at the individual scale that respond to or interact with the environment along a continuum of ecological response and effect.

- **Response trait:** A functional trait that influences the fitness and organismal performance of the individual (Lavorel and Garnier 2002).
- **Effect trait:** A functional trait that influences the fitness and/or organismal performance of an interacting partner and/or ecosystem services and processes (Lavorel and Garnier 2002).

Functional analogues: Traits that are functionally comparable between two or more taxa and that capture both the relevant ecological phenomena and the relevant community assembly process(es) studied

Community assembly processes (Vellend 2016):

- **Speciation:** A way to identify the diversification and history of clades. The importance of including speciation in studies of community assembly tends to increase with spatial and temporal extent, though this depends on the research question.
- **Selection:** Deterministic drivers of species persistence (e.g. environmental tolerance, competitive superiority) that result from fitness differences between individuals or species.
- **Ecological Drift:** Changes in the abundance of different organisms or species due to demographic stochasticity (i.e. chance events).
- **Dispersal:** The movement of organisms or species across space. This is not the same as migration or immigration, as it relates to permanent, non-seasonal residency.

multiple, potentially conflicting trait data handbooks from which to refer. Although it is logical for methodologies to originate within specific taxonomic groups, disagreement across taxonomic standards can result in non-congruent comparisons. For example, multiple ecosystem processes are known to influence body size and other traits in invertebrates (de Bello et al. 2010), making it difficult to isolate the mechanisms that are directly or indirectly related with this trait. In contrast, vertebrate functional ecologists tend to rely heavily on the use of body mass (Ahumada et al. 2011, Heinen et al. 2018, Cooke et al. 2019) due to its wide availability and known links with other important ecological traits that may otherwise be difficult to capture (Cooke et al. 2019). These differing approaches in the collection and management of trait data can challenge the identification of broad trends in functional traits in meta-analyses, as well as the selection of traits for empirical studies across taxa.

Testing links between functional traits and environmental drivers across taxonomic groups can also be problematic (Petchey and Gaston 2006). Invertebrate and plant ecologists have well-established protocols and traits to select from when designing experiments, driven by foundational work linking function to ecological theory (Cummins 1974, Grime 1974). For example, plant functional traits predominantly exist along three dimensions: 1) the attainment and use of resources (e.g. traits along the leaf economics spectrum (Wright et al. 2004)), 2) competitive ability (e.g. plant height) and 3) the potential for regeneration (e.g. seed mass) (Westoby 1998, Westoby et al. 2002, Garnier et al. 2016). Plant ecologists can therefore use an established set of protocols for the measurement and analysis of traits that respond to these three categories (Cornelissen et al. 2003, Pérez-Harguindeguy et al. 2013).

For those outside of plant or invertebrate ecology, deciding which traits to incorporate in their research is less established and more open to researcher selection. Options for trait selection in understudied groups include selecting traits that others have used in their field (if available), selecting traits that are known to be functional in other taxa or reviewing a trait handbook or database (if available). Researchers studying functional traits in less-established taxa may be further challenged by distinguishing among the abundance of functional trait definitions (Table 1). Similarly, traits for taxa that lack trait data standards may not be as robust to divergent definitions and research questions as they are in plants and invertebrates. For example, vertebrate ecologists often include traits or functional groups that reflect behavior (e.g. activity pattern, social structure, behavioral plasticity, diet, habitat preference and locomotion (Ahumada et al. 2011, Santos and Cheylan 2013, Dehling et al. 2014, Wilman et al. 2014, Santini et al. 2019)). However, it is unclear whether these traits are good predictors of ecological conditions (Petchey and Gaston 2006).

Functional comparisons across taxa have increased over the last ten years (Flynn et al. 2009, Moretti and Legg 2009, Vandewalle et al. 2010, Van Der Plas et al. 2012, Aubin et al. 2013, Pedley and Dolman 2014, Lefcheck and Duffy 2015, Heinen et al. 2018). By testing functional responses of broad taxonomic groups (e.g. plants versus insects or birds versus mammals versus reptiles) as opposed to within taxonomic groups, many seek to identify large-scale ecological trends, such as response to disturbance (Flynn et al. 2009, Moretti and Legg 2009, Vandewalle et al. 2010, Aubin et al. 2013, Pedley and Dolman 2014). To select traits for taxonomic comparisons, researchers often focus on traits reflective of environmental conditions. However, difficulties remain in comparing traits in taxa for which metrics diverge

Table 1. Definitions of 'functional trait' in foundational functional ecology literature. Definitions were taken directly from the referenced texts, and categorization of trait type (i.e. response or effect) was determined by the authors following Lavorel and Garnier (2002)'s response and effect trait framework. The number of citations was determined on Google Scholar (<https://scholar.google.com/>) on July 29, 2019.

Publication	Defines functional trait as:	Response or effect	Citations
Tilman (2001)	'… organismal traits that influence ecosystem functioning'	Effect	639
Díaz and Cabido (2001)	'the characteristics of an organism that are considered relevant to its response to the environment and/or its effects on ecosystem functioning'	Response and Effect	2358
Lavorel and Garnier (2002)	'… Response groups and effect groups … Physiological, harder traits at the individual level are more commonly used for effect groups … Whereas response groups are identified through community-level studies of changes in soft, morphological or behavioural traits in response to abiotic or biotic factors'	Response and Effect	2236
McGill et al. (2006)	'a well-defined, measurable property of organisms, usually measured at the individual level and used comparatively across species … that strongly influences organismal performance'	Response	2751
Petchey and Gaston (2006)	'… components of an organism's phenotype that influence ecosystem level processes'	Effect	1544
Violle et al. (2007)	'Any trait which impacts fitness indirectly via its effects on growth, reproduction and survival'	Response	2143
Díaz et al. (2013)	'… morphological, biochemical, physiological, structural, phenological or behavioral characteristics that are expressed in phenotypes of individual organisms and are considered relevant to the response of such organisms to the environment and/or their effects on ecosystem properties'	Response and Effect	263

(as identified by Aubin et al. 2013), as well as in drawing comparisons across varying resolutions of trait data (e.g. individual measures versus species mean traits, see discussion in Lefcheck et al. 2015). With community ecology's long-term goal of identifying generalizable rules in community assembly, particularly across contexts (Lawton 1999), a systematic approach for the selection of traits when conducting cross-taxa functional comparisons is needed.

Synthesizing definitions and unifying approaches

Aligning definitions

To support the selection of traits that reflect ecological reality within and across taxa, we advocate beginning from a broad trait definition. We define functional traits as aspects of phenotypes at the individual scale that exist along a continuum of response and effect. Response traits are phenotypic components that respond to the environment by influencing fitness and organismal performance, while effect traits influence the fitness and/or organismal performance of an interacting partner and/or have an effect upon the environment (Lavorel and Garnier 2002). Functional traits can be physiological, morphological or behavioral. Many functional trait definitions focus on an organism's response to, and therefore fitness, adaptation and organismal performance within, a given ecological context (Calow 1987, McGill et al. 2006, Díaz et al. 2013). However, it can be difficult to quantify traits that correspond with organismal performance (see discussion on performance currencies in McGill et al. 2006) and many trait definitions do not include impacts on performance as a requisite for functionality (Table 1). Discrepancies in trait definitions may be due

in part to researcher focus on effect traits, which most often reflect ecosystem health and processes as opposed to fitness and performance (Lavorel and Garnier 2002, Díaz et al. 2013). Significant work throughout the literature discusses this dichotomy between response and effect traits (Díaz and Cabido 2001, Lavorel and Garnier 2002, Violle et al. 2007, Díaz et al. 2013, Nock et al. 2016). Since the hierarchical filtering of traits mediates the formation of ecological communities (Morin 2011, Aronson et al. 2016), for cross-taxa comparisons we recommend the use of response traits that incorporate organismal performance and fitness relative to ecological filters and assembly processes. However, we also advocate identifying where along the response–effect continuum a given trait lies, as feedbacks between individuals, interacting partners and the ecosystem can have cascading impacts on community assembly (Suding et al. 2008, Sterk et al. 2013).

Ideally, for each considered response trait, investigators will also confirm the trait's adaptability and, if seeking to identify trends through time or the generality of a particular trait–environment relationship, the trait's heritability (see Geber and Griffen 2003, Mitchell 2004, Crisp and Cook 2012 and Garnier et al. 2016 for further discussion on heritability). However, it is often difficult to determine if a trait is adaptive or heritable without lengthy observation and/or experimentation (Dohm 2002, Mitchell 2004). Also, for behavioral traits, heritability may be defined socially or differ depending on scale (e.g. in a family unit versus in a population versus across populations). While identifying when and how traits are adaptive or heritable is useful, especially for evolutionary studies, it may be unrealistic for comparative functional ecology research (see Discussion in de Bello et al. 2015). Nonetheless, we recommend that researchers consider the adaptability or heritability of traits before trait selection, if possible.

Trait selection

Trait significance can vary with environmental context, population or demographic structure. Ensuring that selected traits are relevant for the considered study system and research question is essential for their applicability and comparability. For cross-taxa comparisons, measured traits should capture the ecological phenomena of interest (Petchey and Gaston 2006). For example, when investigating how plant and animal traits change along an elevation gradient, the study should target traits that specifically influence or respond to changes in elevation. However, many studies vary in how they approach trait selection and analysis (Pakeman 2014, Zhu et al. 2017). Similarly, studies may only include a few traits that are easy to measure without describing how these traits directly correspond to the research question or ecological processes (see Discussion in Brousseau et al. 2018).

One approach to select traits for cross-taxa comparisons is to use morphological analogues, or traits that are structurally similar across taxa. However, morphological analogues are not always ecologically equivalent. For example, plant height is often studied due to its correspondence with competitive ability (Garnier et al. 2016). However, height – or rather, body size – in terrestrial invertebrates may correspond more strongly to fecundity (Fountain-Jones et al. 2015) or resource use (Moretti et al. 2017) than competitive ability. Significance of trait–environment relationships may also vary within taxonomic groups. As such, comparing traits by their morphological analogues, even within a single taxonomic group, may result in non-congruent comparisons. We instead advocate considering traits that are functional for a given ecological question when conducting functional trait analyses across taxa (Fig. 1). For example, a researcher interested in how dispersal strategies vary between two communities might select traits that reflect dispersal ability across taxa, regardless of whether these traits are morphologically equivalent. Though this approach often precludes pairwise comparisons, it facilitates broad generalizations and ecological inference across taxa.

Drawing comparisons

Through community-wide, cross-taxonomic comparisons of functional traits, we can improve our understanding of how environmental conditions shape community assembly processes. Since species in the same ecological community
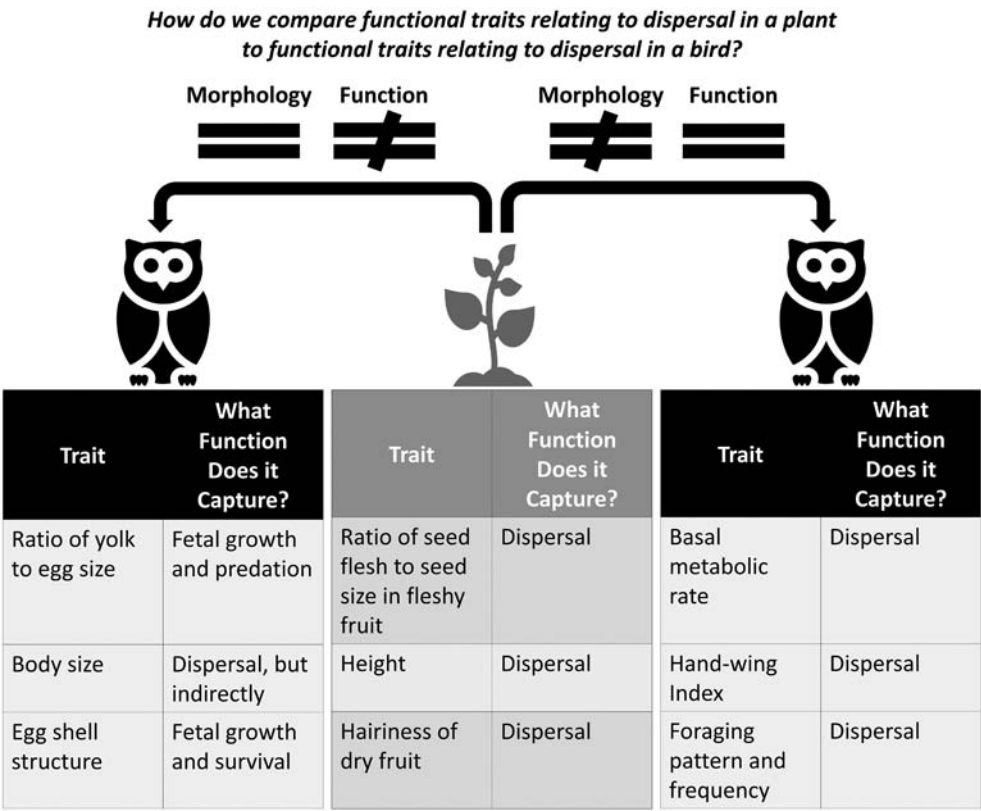

Figure 1. Illustrating the use of functional analogues. Functional traits for plant dispersal (middle gray box) are compared to morphological analogues (traits on the left) and functional analogues (traits on the right) in a bird. Although the morphological analogues represented on the left are structurally equivalent, they do not capture similar functions. The bird functional analogues on the right, however, have equivalent functions to the plant despite differing in morphology. While each trait may correspond with more functions than featured here, we argue that research groups should focus on the function of interest (in this case, dispersal), as opposed to all the functions a trait might capture.

share abiotic and biotic space, they often share fitness constraints (Vellend 2016), and thus commonalities in functional trait response to environmental conditions are expected across taxa. General trait–community relationships have already been found in response to some ecological gradients (e.g. Bergmann's rule for latitudinal gradients (Blackburn et al. 1999) and shifts in body size in response to insularity, as seen in island gigantism (Lomolino 1985, Wesener and Vandenspiegel 2009, Jaffe et al. 2011)). However, limitations imposed on organisms by their evolutionary history can increase or reduce trait divergence between species relative to expectations from the environment alone (see Discussion in Cooke et al. 2019). Further, species occurrence is not driven solely by physiological, morphological and behavioral characteristics, but also community dynamics (e.g. priority effects, inter- and intra-specific interactions, metacommunity dynamics, etc. (Fukami 2010)). Therefore, to understand how environments filter particular traits across taxa to form ecological communities, we recommend considering the response of a broad set of relevant traits for each taxa to specific community assembly processes (i.e. speciation, selection, ecological drift, dispersal (Vellend 2016)).

As an example of our method, we will use a hypothetical study in which a researcher wishes to determine if there is a measurable functional response to elevation in both plant and bird communities. ==We first suggest defining the specific scope of the project by considering which traits most strongly correspond with a given community assembly mechanism for the study system.== For traits related to dispersal, for example, the researcher might select for plants: height, seed size, mode of dispersal, etc. and for birds: basal metabolic rate, hand-wing index, foraging pattern and frequency, etc. This list should include all traits associated with or sensitive to the community assembly process at an appropriate comparative scale, such as a sub-alpine versus alpine community. We next recommend considering whether it is feasible to collect the necessary trait data. For some taxa, such as larger vertebrates, direct measurement of traits, such as body mass, may be difficult. In such instances, one may choose to use species-averages. However, if comparing individual-level to species- or higher-level trait data, we suggest the use of data reduction techniques, such as averaging, to ensure that comparisons are of similar resolution. We further recommend that researchers select traits that interact with the environment at similar spatial scales to ensure that the underlying fitness constraints are comparable. Upon completion of these steps, the researcher could then assess whether traits associated with dispersal increase or vary predictively in both bird and plant communities along an elevation gradient.

If functional traits across a given set of taxa are not easy to measure, lack a reliable proxy for quantification or are not comparable, various techniques may help address these issues. If only a small amount of data is missing, imputation may help to fill data gaps (Cooke et al. 2019). If data are prohibitively limited, we recommend checking whether other kinds of data could capture the desired functional traits. These data

should reflect a facet of an organism that contributes to its persistence in an ecological community, such as demographic rates (Salguero-Gómez et al. 2018) or ecological strategies (e.g. fast versus slow life history). If selecting a proxy for functional traits is not possible, then functional trait approaches might not be suitable, and the researcher may want to consider alternative methods (see Additional considerations).

Our method provides a means of testing for directional shifts in community assembly processes across ecological communities and along spatial and temporal gradients. Since we recommend comparing data of similar resolution (e.g. species-to species-level) which are united by function as opposed to morphology or phenotype, our approach also allows for the comparison of multiple units, trait types and trait classes. Many authors have provided suggestions and guidance for terminology standardization and approaches for functional comparisons within and across taxa (Petchey and Gaston 2006, Fountain-Jones et al. 2015, Lefcheck et al. 2015, Schmera et al. 2015, Brousseau et al. 2018). However, most approaches focus on specific taxonomic groups or ecosystems, and often do not explicitly link selected traits to community assembly (but see Brousseau et al. 2018). Our approach builds on previous work (Brousseau et al. 2018) to link environmental filtering to cross-taxonomic drivers of assembly.

When comparing community assembly across taxa, we advocate for the selection of functionally analogous traits associated with community assembly processes. Petchey and Gaston (2006) similarly provide suggestions for how to collect trait data based on functional relevance for a given research question. However, the ecological underpinnings of plant functional ecology do not always transfer well to other taxonomic disciplines (Kissling et al. 2018), limiting our ability to identify functionally relevant traits in understudied taxa. Grounding trait selection explicitly in community assembly may better incorporate understudied taxa in functional trait research and comparative ecology.

Conceptual limitations

By using a functionally analogous approach that focuses on the processes that shape ecological communities, researchers can better ascertain mechanisms of community assembly across taxa. However, for certain taxa and across particular spatio-temporal scales, comparisons may not be realistic. For example, ==microbes and birds interact with the environment at starkly different scales, although their geographic distributions may overlap.== Additionally, since functionally analogous traits may be expressed in different units and at different scales, ==we do not recommend drawing direct one-to-one comparisons of traits across taxa. Instead, we advocate comparing directional shifts of functionally analogous traits across environmental gradients and communities to identify trends in community assembly== (Fig. 1). In this way, our method supports the identification of traits that correspond with drivers of ecosystem and community change, such as abiotic gradients, urbanization, invasion and climate change.

Additional considerations

After linking selected traits with community assembly processes, researchers may also address the following considerations:

- Are there feedbacks between the selected traits and the community assembly process(es)?
- Does the significance of selected traits shift across the study system in response to changes in the environment or to community assembly?
- When considering response and effect traits along a continuum (i.e. a trait that influences individual fitness, organismal performance and ecosystem processes (Lavorel and Garnier 2002)), are there feedbacks between the environment and selected traits that impact the relative importance of each?
- Are there opportunities to link traits to demographic rates (Salguero-Gómez et al. 2018), behavioral syndromes, competition (Cadotte and Tucker 2017), trophic position (de Bello et al. 2010, Fountain-Jones et al. 2017) or other data to provide a more nuanced and three-dimensional view of how communities assemble in a given study area?
- Do the responses of selected traits differ depending upon the study scale? Are considerations across scales important to answer a given research question?

Despite its over thirty-year history within the literature, functional trait approaches are still evolving, especially across environmental contexts and in understudied taxa (Kissling et al. 2018). Incorporating other datasets (e.g. demography (Salguero-Gómez et al. 2018)) can provide a more holistic view of what is occurring in an ecological community. Using functional traits as one of the many tools available to capture community and environmental complexity will help improve the generality of functional comparisons.

Discussion and future directions

We provide conceptual methods for cross-taxa comparisons of response traits to understand broad trends in community assembly. However, there is also a need to create protocols, standards and conceptual methods for the selection and comparison of other kinds of trait data. Effect traits are increasingly used to identify how global change influences the roles that organisms play within their environment to support ecosystem service provisioning and resilience (Cardinale et al. 2012, Funk et al. 2017). In a world of growing conservation need, identifying clear standards for the collection, collation and use of effect trait data across taxa will facilitate the identification of drivers of ecosystem service provisioning.

Since human facilitation and landscape legacies contribute to the hierarchical filtering of species traits in the Anthropocene (Aronson et al. 2016), trait distributions may become increasingly shaped by human value-systems (Williams et al. 2009, Lavorel and Grigulis 2012). By identifying the traits people

prefer or find harmful, we can link human preference to community assembly in human-dominated systems. Including traits that are sensitive to human activities or that account for human selection of certain phenotypes could support more accurate representations of species distributions and responses to global change. However, best practices for the incorporation of human-mediated trait data are still under development (Goodness et al. 2016). Continued advancements in the ecological literature will need to provide clearer approaches for integrating different kinds of trait data to ensure consistent comparisons.

Conclusions

With new technology, increased data availability and interdisciplinary collaboration, our understanding of interactions between organisms and the environment is constantly refined. We anticipate these advances will provide clearer linkages between ecological processes and the functional traits they mediate. Increased collaboration between sub-disciplines in functional ecology will facilitate the identification of general functional trait–environment relationships across taxa. Comparing functionally analogous traits that relate to community assembly processes can reveal whether trait–environment relationships differ between, and even within, taxonomic groups. While cross-taxa comparisons may not always be feasible or meaningful depending on the system and scale, by focusing broadly across taxa, we may approach generalizability in community assembly and its requisite processes.

References

Ahumada, J. A. et al. 2011. Community structure and diversity of tropical forest mammals: data from a global camera trap network. – Phil. Trans. R. Soc. B 366: 2703–2711.

Altermatt, F. et al. 2015. Big answers from small worlds: a user's guide for protist microcosms as a model system in ecology and evolution. – Methods Ecol. Evol. 6: 218–231.

Aronson, M. F. J. et al. 2016. Hierarchical filters determine community assembly of urban species pools. – Ecology 97: 2952–2963.

Aubin, I. et al. 2013. Can a trait-based multi-taxa approach improve our assessment of forest management impact on biodiversity? – Biodivers. Conserv. 22: 2957–2975.

Blackburn, T. I. M. M. et al. 1999. Geographic gradients in body size: a clarification of Bergmann's rule. – Divers. Distrib. 5: 165–174.

Blonder, B. 2017. Hypervolume concepts in niche- and trait-based ecology. – Ecography 41: 1441–1455.

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.

Cadotte, M. W. and Tucker, C. M. 2017. Should environmental filtering be abandoned? – Trends Ecol. Evol. 32: 429–437.

Calow, P. 1987. Towards a definition of functional ecology. – Funct. Ecol. 1: 57–61.

Cardinale, B. J. et al. 2012. Biodiversity loss and its impact on humanity. – Nature 486: 59–67.

Chapin, S. F. et al. 2000. Consequences of changing biodiversity. – Nature 405: 234–242.

Cooke, R. S. C. et al. 2019. Projected losses of global mammal and bird ecological strategies. – Nat. Commun. 10: 2279.

Cornelissen, J. H. C. A. et al. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. – Aust. J. Bot. 51: 335–380.

Crisp, M. D. and Cook, G. 2012. Phylogenetic niche conservatism: what are the underlying evolutionary and ecological causes? – New Phytol. 196: 681–694.

Cummins, K. W. 1974. Structure and function of stream ecosystems. – Bioscience 24: 631–641.

Dawson, S. K. et al. 2019. Handbook for the measurement of macrofungal functional traits: a start with basidiomycete wood fungi. – Funct. Ecol. 33: 372–387.

de Bello, F. et al. 2010. Towards an assessment of multiple ecosystem processes and services via functional traits. – Biodivers. Conserv. 19: 2873–2893.

de Bello, F. et al. 2015. On the need for phylogenetic 'corrections' in functional trait-based approaches. – Folia Geobot. 50: 349–357.

Degen, R. et al. 2018. Trait-based approaches in rapidly changing ecosystems: a roadmap to the future polar oceans. – Ecol. Indic. 91: 722–736.

Dehling, D. M. et al. 2014. Functional and phylogenetic diversity and assemblage structure of frugivorous birds along an elevational gradient in the tropical Andes. – Ecography 37: 1047–1055.

Díaz, S. and Cabido, M. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. – Trends Ecol. Evol. 16: 646–655.

Díaz, S. et al. 2013. Functional traits, the phylogeny of function, and ecosystem service vulnerability. – Ecol. Evol. 3: 2958–2975.

Dohm, M. R. 2002. Repeatability estimates do not always set an upper limit to heritability. – Funct. Ecol. 16: 273–280.

Flynn, D. F. B. et al. 2009. Loss of functional diversity under land use intensification across multiple taxa. – Ecol. Lett. 12: 22–33.

Fountain-Jones, N. M. et al. 2015. Moving beyond the guild concept: developing a practical functional trait framework for terrestrial beetles. – Ecol. Entomol. 40: 1–13.

Fountain-Jones, N. M. et al. 2017. Trophic position determines functional and phylogenetic recovery after disturbance within a community. – Funct. Ecol. 31: 1441–1451.

Frenette-Dussault, C. et al. 2013. Linking plant and insect traits to understand multitrophic community structure in arid steppes. – Funct. Ecol. 27: 786–792.

Fukami, T. 2010. Community assembly dynamics in space. – In: Verhoef, H. A. and Morin, P. J. (eds), Community ecology: processes, models, and applications. Oxford Univ. Press, pp. 45–54.

Funk, J. L. et al. 2017. Revisiting the Holy Grail: using plant functional traits to understand ecological processes. – Biol. Rev. 92: 1156–1173.

Garnier, E. et al. 2016. Plant functional diversity. – Oxford Univ. Press.

Geber, M. A. and Griffen, L. R. 2003. Inheritance and natural selection on functional traits. – Int. J. Plant Sci. 164: S21–S42.

Goodness, J. et al. 2016. Exploring the links between functional traits and cultural ecosystem services to enhance urban ecosystem management. – Ecol. Indic. 70: 597–605.

Grime, J. P. 1974. Vegetation classification by reference to strategies. – Nature 250: 26–31.

Heinen, J. H. et al. 2018. Extinction-driven changes in frugivore communities on oceanic islands. – Ecography 41: 1245–1255.

Jaffe, A. L. et al. 2011. The evolution of island gigantism and body size variation in tortoises and turtles. – Biol. Lett. 7: 558–561.

Jarzyna, M. A. and Jetz, W. 2018. Taxonomic and functional diversity change is scale dependent. – Nat. Commun. 9: 1–8.

Keddy, P. A. 1992. A pragmatic approach to functional ecology. – Funct. Ecol. 6: 621–626.

Kimball, S. et al. 2016. Can functional traits predict plant community response to global change? – Ecosphere 7: e01602.

Kissling, W. D. et al. 2018. Towards global data products of essential biodiversity variables on species traits. – Nat. Ecol. Evol. 2: 1531–1540.

Laureto, L. M. O. et al. 2015. Functional diversity: an overview of its history and applicability. – Nat. Conserv. 13: 112–116.

Lavorel, S. and Garnier, E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. – Funct. Ecol. 16: 545–556.

Lavorel, S. and Grigulis, K. 2012. How fundamental plant functional trait relationships scale-up to trade-offs and synergies in ecosystem services. – J. Ecol. 100: 128–140.

Lavorel, S. et al. 2007. Plant functional types: are we getting any closer to the Holy Grail? – In: Canadell, J. et al. (eds), Terrestrial ecosystems in a changing world. Springer, pp. 171–186.

Lawton, J. H. 1999. Are there general laws in ecology? – Oikos 84: 177–192.

Lebrija-Trejos, E. et al. 2010. Functional traits and environmental filtering drive community assembly in a species-rich tropical system. – Ecology 91: 386–398.

Lefcheck, J. S. and Duffy, E. J. 2015. Multitrophic functional diversity predicts ecosystem functioning in experimental assemblages of estuarine consumers. – Ecology 96: 2973–2983.

Lefcheck, J. S. et al. 2015. Choosing and using multiple traits in functional diversity research. – Environ. Conserv. 42: 104–107.

Lomolino, M. V. 1985. Body size of mammals on islands: the island rule reexamined. – Am. Nat. 125: 310–316.

McGill, B. J. et al. 2006. Rebuilding community ecology from functional traits. – Trends Ecol. Evol. 21: 178–185.

Mitchell, R. J. 2004. Heritability of nectar traits: why do we know so little? – Ecology 85: 1527–1533.

Moretti, M. and Legg, C. 2009. Combining plant and animal traits to assess community functional responses to disturbance. – Ecography 32: 299–309.

Moretti, M. et al. 2017. Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. – Funct. Ecol. 31: 558–567.

Morin, P. J. 2011. Community ecology. – Wiley-Blackwell.

Mouillot, D. et al. 2013. A functional approach reveals community responses to disturbances. – Trends Ecol. Evol. 28: 167–177.

Nock, C. A. et al. 2016. Functional traits. – eLS: 1–8, doi: 10.1002/9780470015902.a0026282.

Pakeman, R. J. 2014. Functional trait metrics are sensitive to the completeness of the species' trait data? – Methods Ecol. Evol. 5: 9–15.

Pedley, S. M. and Dolman, P. M. 2014. Multi-taxa trait and functional responses to physical disturbance. – J. Anim. Ecol. 83: 1542–1552.

Pérez-Harguindeguy, N. et al. 2013. New handbook for standardised measurement of plant functional traits worldwide. – Aust. J. Bot. 61: 167–234.

Perronne, R. et al. 2017. How to design trait-based analyses of community assembly mechanisms: insights and guidelines from a literature review. – Perspect. Plant Ecol. Evol. Syst. 25: 29–44.

Petchey, O. L. and Gaston, K. J. 2006. Functional diversity: back to basics and looking forward. – Ecol. Lett. 9: 741–758.

Pey, B. et al. 2014. A thesaurus for soil invertebrate trait-based approaches. – PLoS One 9: e108985.

Poff, N. L. et al. 2006. Functional trait niches of North American lotic insects: traits-based ecological applucations in light of phylogenetic relationships. – J. North Am. Benthol. Soc. 25: 730–755.

Salguero-Gómez, R. et al. 2018. Delivering the promises of trait-based approaches to the needs of demographic approaches, and vice versa. – Funct. Ecol. 32: 1424–1435.

Santini, L. et al. 2019. One strategy does not fit all: determinants of urban adaptation in mammals. – Ecol. Lett. 22: 365–376.

Santos, X. and Cheylan, M. 2013. Taxonomic and functional response of a Mediterranean reptile assemblage to a repeated fire regime. – Biol. Conserv. 168: 90–98.

Schmera, D. et al. 2015. A proposed unified terminology of species traits in stream ecology. – Freshwater Sci. 34: 823–830.

Schneider, F. D. et al. 2018. Towards an ecological trait-data standard. – bioRxiv: 1–28, preprint at: <www.biorxiv.org/content/early/2018/03/31/328302>.

Sterk, M. et al. 2013. Assess ecosystem resilience: linking response and effect traits to environmental variability. – Ecol. Indic. 30: 21–27.

Suding, K. N. and Goldstein, L. J. 2008. Testing the Holy Grail framework: using functional traits to predict ecosystem change. – New Phytol. 180: 559–562.

Suding, K. N. et al. 2008. Scaling environmental change through the community-level: a trait-based respanse-and-effect framework for plants. – Global Change Biol. 14: 1125–1140.

Tilman, D. 2001. Functional diversity. – In: Levin, S. A. (ed.), Encyclopedia of biodiversity, 3rd edn. Academic Press, pp. 109–120.

Tscharntke, T. et al. 2008. Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. – Ecology 89: 944–951.

Van Der Plas, F. et al. 2012. Trait similarity patterns within grass and grasshopper communities: multitrophic community assembly at work. – Ecology 93: 836–846.

Vandewalle, M. et al. 2010. Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. – Biodivers. Conserv. 19: 2921–2947.

Vellend, M. 2016. The theory of ecological communities, SA Levin and HS Horn (eds). – Princeton Univ. Press.

Violle, C. et al. 2007. Let the concept of trait be functional! – Oikos 116: 882–892.

Wesener, T. and Vandenspiegel, D. 2009. A first phylogenetic analysis of Giant Pill–Millipedes (Diplopoda: Sphaerotheriida), a new model Gondwanan taxon, with special emphasis on island gigantism. – Cladistics 25: 545–573.

Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. – Plant Soil 199: 213–227.

Westoby, M. et al. 2002. Plant ecological strategies: some leading dimensions of variation between species. – Annu. Rev. Ecol. Syst. 33: 125–159.

Williams, N. S. G. et al. 2009. A conceptual framework for predicting the effects of urban environments on floras. – J. Ecol. 97: 4–9.

Wilman, H. et al. 2014. EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. – Ecology 95: 2027.

Wright, I. J. et al. 2004. The worldwide leaf economics spectrum. – Nature 428: 821–827.

Zhu, L. et al. 2017. Trait choice profoundly affected the ecological conclusions drawn from functional diversity measures. – Sci. Rep. 37: 1–13.