Animal functional traits: towards a trait-based ecology for whole ecosystems

Matthias Schleuning[1], Daniel García[2], Joseph A. Tobias[3]

[1]Senckenberg Biodiversity and Climate Research Centre (SBiK-F), Senckenberganlage 25, 60325 Frankfurt (Main), Germany. Email: matthias.schleuning@senckenberg.de

[2] Departamento Biología de Organismos y Sistemas (Universidad de Oviedo) and Instituto Mixto de Investigación en Biodiversidad (Universidad de Oviedo-CSIC-Principado de Asturias), Oviedo, Spain

[3]Department of Life Sciences, Imperial College London, Silwood Park, Ascot SL5 7PY, UK

Funding information

Not applicable

Conflict of interest

M.S., D.G. and J.A.T. are Associate Editors of Functional Ecology, but took no part in the peer review and decision-making processes for this paper.

Data availability statement

No data were used for this Editorial.

Author contributions

All authors contributed equally to sketching the outline of the Editorial. M.S. wrote the first manuscript draft, all authors contributed to further revisions and the final manuscript.

Acknowledgements

We thank all contributing authors and the editorial team at Functional Ecology for greatly supporting the preparation and compilation of this Special Focus. Jörg Albrecht, Enrico Rezende and Emma Sayer commented on a draft of this Editorial and helped to improve its structure and clarity.

Abstract

1. Functional traits and associated trait-based concepts have driven rapid innovation in ecology over recent years, with most progress based on insights from plants. However, plants are almost entirely restricted to a single trophic level, an over-reliance on plant traits, thus, neglects the complexity of biotic interactions across trophic levels and their importance for community assembly and ecosystem functioning.

2. The need to expand the focus of trait-based ecology across trophic levels has led to an upsurge in attention on animal functional traits and the emergence of new concepts relevant to community ecology, macroecology and ecosystem science. Recent progress in the compilation of global trait datasets for some taxa has opened up new possibilities for testing macroecological theory.

3. In this Special Focus, we explore how trait-based ecology can contribute to expand insights from single to multiple trophic levels, how these insights can be used to upscale understanding from local communities to biogeographic patterns, and how this can ultimately help to predict the impacts of global change on ecosystem functions. To address these key questions, we showcase studies on diverse animal taxa ranging in size from springtails to crocodiles and spanning multiple trophic levels from primary consumers to apex predators.

4. This collection of studies shows how precise measurements of morphological or physiological traits can increase mechanistic understanding of community assembly across trophic levels. In particular, it is demonstrated how trait-based analyses help to identify mechanisms that underpin large-scale biodiversity patterns. Further, a clearer picture is emerging of systematic animal responses to environmental change that shape the trait composition of ecological communities and affect ecosystem functioning.

5. The articles in this volume highlight the need to move trait-based ecology beyond the limits of taxonomic boundaries. The integration of trait data and concepts across trophic levels opens up new possibilities for identifying general ecological mechanisms that shape patterns and processes operating at different scales. The identification of key functional traits and their interplay across trophic levels can underpin the development of a trait-based ecology for whole ecosystems, which could eventually enable predictions of the ecosystem-level consequences of biodiversity loss.

Keywords

Community assembly, ecological networks, ecosystem functioning, functional biogeography, macroecology, species coexistence, trait-based concepts, trophic interactions.

Introduction

Ecological research centres on the question of how organisms interact with their environment and with other organisms (McGill et al., 2006). The identification of processes underpinning these interactions is key to move from the description of ecological processes towards mechanistic understanding and prediction (Funk et al., 2017). One of the most promising ways to gain such a mechanistic understanding are trait-based concepts (McGill et al., 2006; Violle et al., 2007). Over the last decades, trait-based ecology has been dominated by plant-based concepts and data (Kattge et al., 2020; Suding et al., 2008) and, thus, focused on processes operating within trophic levels (Kraft et al., 2008; Mason et al., 2011). However, these advances often neglect the key role of interactions across trophic levels for understanding and predicting patterns and processes at the level of whole ecosystems (Schmitz et al., 2015; Seibold et al., 2018). The need to expand trait-based ecology from single to multiple trophic levels has promoted recent development of comprehensive datasets of animal functional traits (Herberstein et al., 2022; Tobias et al., 2022).

Functional traits are the measurable properties of organisms that influence organismal performance via their effects on individual growth, survival and reproduction (Violle et al., 2007) and thereby determine how organisms respond to their abiotic and biotic environment and contribute to ecological processes and ecosystem functions (Suding et al., 2008). Using functional traits to generalize ecological understanding from single taxa to entire communities has had a big impact on ecological research over the last two decades (Funk et al., 2017; Lavorel & Garnier, 2002) and led to the identification of core principles in community ecology and ecosystem science. For instance, plant-centred studies have shown that trait divergence determines competitive interactions between species and shapes processes of community assembly and species coexistence (Kraft et al., 2008; Mason et al., 2011). Moreover, trait-based trade-offs determine strategies of resource acquisition and processing (Reich, 2014) and structure variation in plant form and function at the global scale (Díaz et al., 2016). Trait-based concepts have also been put into the context of ecosystem science. A key concept based on the distinction between functional response and effect traits states that both the responses of species to environmental variation and their effects on ecological processes determine the relationship between biodiversity and ecosystem functioning (Díaz et al., 2013; Suding et al., 2008). So far, these insights into community assembly and ecosystem functioning have mostly been derived from studies of plant-plant interactions, plant responses to abiotic factors, and plant effects on biomass accumulation and ecosystem productivity (Enquist et al., 2020; Funk et al., 2017). The complexity of ecosystems, however, can only be uncovered if trait-based concepts contribute to a mechanistic understanding of the biotic interrelationships and dependencies across trophic levels (Fig. 1).

Trait-based approaches can indeed aid the identification of interaction rules between species located at different trophic levels (Fig. 1). For instance, studies of mutualistic networks have demonstrated that the shape of a flower determines which animal species are able to access its nectar (Dalsgaard et al., 2021; Maglianesi et al., 2014), while body size defines the vulnerability of an organism to a predator species in food webs (Stouffer et al., 2011; Brose et al., 2017). Importantly, trait relationships across trophic levels do not only determine the flux of energy from lower to upper trophic levels, but also have important feedback effects onto lower trophic levels through ecosystem functions such as pollination, seed dispersal and decomposition (Fig. 1). Trait-matching frameworks have mostly been derived from the analysis of ecological networks (Bartomeus et al., 2016; Schleuning et al., 2015) and complemented seminal concepts that were primarily derived from the plants' perspective (Lavorel et al., 2013).

We are currently entering a new era of open science providing access to trait data with rapidly increasing coverage within and across taxonomic groups (Gallagher et al., 2020). Given this upsurge of data, trait-based approaches have the potential to be a game-changer in ecological research and could lead to new mechanistic insights into organismal form-function relationships structuring whole ecosystems. However, these advances cannot be taken for granted, in particular if there is a gap between data availability and the concurrent conceptual and methodological advances in trait-based ecology. So far, trait-based studies of animals mostly rely on easily measurable traits, such as organismal size, or widely available *soft* traits, such as the ecological preferences of species (Jones et al., 2009; Wilman et al., 2014), both of which may only have weak and indirect effects on the ecological processes under study (Funk et al., 2017). Moreover, trait-based ecology has been biased towards species-poor ecosystems (Etard et al., 2020) and to taxonomic groups in which the relationship between organismal form and function may be particularly tight, such as plants (Díaz et al., 2016) and birds (Pigot et al., 2020). The capacity of trait-based approaches to generalize ecological understanding across trophic levels and spatial scales therefore remains to be tested for most animal taxa and ecosystems.

Key questions of the Special Focus

With this Special Focus, we gauge the state of the art in research on animal functional traits and associated concepts. We aim to cover the broadest possible range of animal taxa in order to address three key questions of trait-based ecology. (Q1) Do functional traits allow us to generalize insights from single to multiple trophic levels? (Q2) Can we use trait-based approaches to upscale understanding from local communities to biogeographic patterns? (Q3) How can trait-based approaches contribute to better predictions of global-change impacts on biodiversity and ecosystem functioning? In the following, we discuss recent scientific progress around these three key questions, with a slight bias towards the topics and taxa covered in this Special Focus.

Question 1. Expanding insights from single to multiple trophic levels

In recent years, trait-based approaches have been applied to taxa from across the tree of life making this a truly universal approach in ecological research (Capdevila et al., 2020; Carmona et al., 2021). The studies presented in this Special Focus cover animal taxa with a body mass ranging from about 0.1 mg to 1000 kg and inhabiting aquatic and terrestrial ecosystems. The featured animal taxa are located at different trophic levels including primary consumers, secondary consumers, apex predators and detritivores (Fig. 1). The diversity of studies across trophic levels demonstrates the great potential of trait-based approaches for gaining a multi-trophic understanding of the assembly of ecological communities (Seibold et al., 2018). Moreover, conceptual progress in trait-based ecology provides means to compare the functional roles of species from different trophic levels (Dehling & Stouffer, 2018) and to identify the key processes shaping trophic interactions (Wootton et al., 2023).

So far, the specific functional traits underpinning ecological processes and ecosystem functions are unknown for most taxa. Moreover, different functional traits may shape species interactions within and across trophic levels (Walter et al., 2023), demonstrating that multiple traits jointly structure multi-trophic communites and ecosystem functions (Gravel et al., 2016). In particular, morphological traits alone may not always be sufficient for predicting trophic interactions and their associated ecosystem functions (Bartomeus et al., 2016). In the Special Focus, it is shown that trophic interactions between plants and animals are not only structured by morphological trait matching, but also depend on the relationship between the energetic demands of animals and the energetic provisions of plants (Neu et al., 2023). The importance of physiological traits in shaping community composition is also shown for dung beetles communities (Williamson et al., 2022). Measurements and analyses of specific functional traits, however, do not necessarily outperform the predictive power of *soft* ecological traits. For instance, the morphological traits of wood-inhabiting beetles were less informative to derive trait-environment associations compared to ecological categorizations of species (Drag et al., 2023). This demonstrates that we as functional ecologists need to continue the quest for the most informative traits. By identifying more and more of these traits, we will eventually be able to fully exploit the possibilities of trait-based ecology and analyse how trait-based processes that operate within and across across trophic levels structure ecological communites.

Question 2. Upscaling understanding from small to large spatial scales

Ecologists strive to generalize understanding from one ecosystem to another and from small to large spatial scales by using functional traits. The identification of such generalities and the foundation of functional biogeography hinges on the availability of global trait datasets (Violle et al., 2014). Recent progress in trait-based ecology demonstrates that the field is rapidly advancing in that direction and that macroecology and functional ecology have started to address similar questions. Many of the studies included in this Special Focus worked on large spatial scales across elevational (Drag et al., 2023) and latitudinal gradients (Ferrín et al., 2023; Ibarra-Isassi et al., 2023; Srivastava et al., 2023), or even covered the entire globe (Ali et al., 2023; Crouch & Jablonski, 2023; Pincheira-Donoso et al., 2023). Importantly, these large-scale analyses are no longer restricted to vertebrates (Etard et al., 2020), but are now also possible for many invertebrate groups including ants, beetles, springtails and aquatic macroinvertebrates.

Based on the insights from such studies, we identify two main benefits derived from trait-based analyses at large spatial scales. First, large-scale studies provide broad environmental gradients and help to detect previously unknown associations between functional traits and environmental conditions. For instance, this has enabled the identification of functional traits mediating springtail responses to aridity and drought (Ferrín et al., 2023) or mechanisms of species sorting according to ant functional traits across forest biomes (Ibarra-Isassi et al., 2023). Second, and even more important, large-scale analyses of trait diversity can be used to test macroecological theory (Lamanna et al., 2014) and assembly rules of ecological communities and networks (Marjakangas et al., 2022). As expected, the findings of such empirical studies are not as straightforward as theory would predict and show that patterns in trait diversity and trait matching across trophic levels are contingent on the biogeographic context (Dalsgaard et al., 2021; Srivastava et al., 2023). As a consequence of such contingencies, macroecological trends and small-scale community responses to changing environmental conditions can be disconnected (Ferrín et al., 2023). Nevertheless, adding functional traits to large-scale analyses of ecological networks generally outperforms the predictive power of analyses merely based on taxonomic entities (Dehling et al., 2021). At a global scale, trait-based approaches can help to detect mechanisms underpinning the latitudinal diversity gradient and explain why tropical ecosystems contain so many more species than ecosystems distant from the equator (Lamanna et al., 2014). For instance, trait-based analyses can be used to infer the intensity of competitive interactions between species and test whether trait divergence differs across ecological communities globally (Crouch & Jablonski, 2023). These first steps on the new ground of functional biogeography are most promising and call for intensified efforts in the compilation of global trait data for many more taxonomic groups (Gallagher et al., 2020). It will be exciting to see how these upcoming efforts will further advance understanding of the mechanisms underlying global biodiversity patterns.

Question 3. Predicting the ecosystem-level consequences of biodiversity loss

One of the biggest promises of trait-based ecology is to generalize ecological understanding from a species-specific perspective towards an ecosystem-level understanding. As a prime example, trait-based ecology has gathered ample evidence that the downsizing of ecological communities by the selective extinction of the largest organisms and their functional traits reduces ecosystem functioning (Dirzo et al., 2014; Enquist et al., 2020; Fricke et al., 2022). The studies in this Special Focus demonstrate that the step from the species to the ecosystem level can now be principally taken for many types of ecosystem functions, such as litter and wood decomposition by springtails and beetles (Drag et al., 2023; Ferrín et al., 2023), pollination and seed predation by birds and insects (Neu et al., 2023), or avian seed dispersal and arthropod predation (Peña et al., 2023). Taking this step by means of trait-based analyses enables ecologists to predict global-change impacts on ecosystem functioning and contributes key knowledge to ecosystem and conservation management.

An important consensus across many previous studies has been that global change leads to systematic losses of species with particular functional traits (Carmona et al., 2021; Clavel et al., 2011; Dirzo et al., 2014). Using trait-based approaches, the studies compiled in this Special Focus infer systematic species responses to global change for very different taxonomic groups of animals. For instance, the thermal sensitivity of dung beetles mediates community responses to temperature increase following deforestation (Williamson et al., 2022), whereas dispersal capacity helps explain occurrence patterns of bats in tropical forest fragments (Colombo et al., 2023). Globally, species extinctions are projected to lead to systematic reductions in the trait space of birds (Ali et al., 2023) and crocodiles (Griffith et al., 2023). In particular, these studies show how species extinctions result in shifts in size-independent trait dimensions such as those related to climatic tolerance, foraging and movement (Ali et al., 2023; Griffith et al., 2023). In amphibians, extinction risk was related to a large body size across amphibian taxa, but was also associated with taxon-specific drivers, such as UV-B radiation increasing the extinction risk for salamanders (Pincheira-Donoso et al., 2023). Systematic changes in community composition are likely to trigger feedback effects on other trophic levels in ecological networks (Bascompte et al., 2019; Schleuning et al., 2016) and on ecosystem functions dependent on trophic interactions (Gravel et al., 2016). However, only few studies have empirically tested how this affects ecosystem functioning in multi-trophic communities (Eisenhauer et al., 2019). This is primarily due to the difficulty of measuring ecosystem functions mediated by interactions across trophic levels. In a study based on empirical measures of avian ecosystem functions, trait-based analyses were most powerful for those functions that are constrained by the trait matching between consumer and resource species (Peña et al., 2023). Further cross-function analyses will be needed to identify the mechanisms by which trait diversity and ecosystem functioning are related across trophic levels (Gagic et al., 2015; Peña et al., 2023), which will be the basis for predicting the consequences of biodiversity loss for whole ecosystems.

Towards the integration of trait data, concepts and knowledge

We have identified three key questions of trait-based ecology and showed how recent work has contributed to start answering these questions. The biggest potential of trait-based ecology emerges from its possibility to synthesize scientific insight from across different branches of the tree of life, for instance by projecting a snail, a beetle and a fox into the same functional trait space (Junker et al., 2023). This potential for generalization can open up unprecedented opportunities for testing ecological theory (Violle et al., 2014) and for applying the gained knowledge to ecosystem and conservation science (Laughlin, 2014). From a multi-trophic perspective, we have only started to move towards these goals and, despite decades of trait-based ecology, only have a fragmentary knowledge biased towards specific taxa and biogeographic regions (Etard et al., 2020). We therefore argue that the future of trait-based ecology will lie in the integration of data, concepts and knowledge.

The asymmetric advances in trait data collection have led to an uneven availability of data across taxa. Plant ecologists have early on identified the big potential of trait-based concepts (Lavorel & Garnier,

2002) and the need for coordinated global efforts of trait data compilation (Kattge et al., 2020). Animal ecology can learn from this experience and start integrating currently disparate data into global trait databases with a high coverage within and across taxa (Gallagher et al., 2020). The parallel integration of trait-based concepts across taxa can be facilitated by recent advances in life-history and metabolic theory (Brown et al., 2018; Healy et al., 2019). Putting these theoretical advances into a trait-based perspective enables new insights into the functional principles structuring plant and animal diversity (Capdevila et al., 2020; Junker et al., 2023). A big strength of such approaches is that they provide a nexus between classic theory (Grime, 1988; Pianka, 1970; Stearns, 1976) and modern tools of trait-based analyses and models (Enquist et al., 2020; Villéger et al., 2008; Wootton et al., 2023). This conceptual integration should not stop at the borders of the plant and animal kingdom, but actually provides ready-to-use pathways for comparative analyses based on universal functional traits applicable to both plants and animals (Carmona et al., 2021; Gibb et al., 2023). Putting plants and animals side by side can yield many unexpected and surprisingly obvious analogies, for instance between the ecological strategies of plants and eusocial insects such as ants (Gibb et al., 2023).

Trait-based ecology has so far focussed on traits that are relatively easy to measure and vary mostly at species rather than at individual level (Herberstein et al., 2022; Tobias et al., 2022). Traits related to animal behaviour that define responses of individual animals to global change (Carlson et al., 2021) are yet underrepresented in global trait datasets, despite the increasing availability of such data, e.g., on animal movements (Kays et al., 2022). Trait-based ecology therefore needs to develop unifying frameworks that are able to integrate trait data describing the phenology, life history, morphology, physiology and behaviour of organisms from across taxonomic groups (Kissling et al., 2018). Such an integration will provide many new opportunities for cross-taxon analyses and increase the capacity to disentangle trait variation and organismal responses to environmental change within and across species (Ibarra-Isassi et al., 2023). Given these big opportunities, the research community is very much aware of the need for trait data integration, the necessity to develop interoperable methods and data protocols (Palacio et al., 2022; Schneider et al., 2019), as well as the synergies emerging from an adherence to open science principles (Gallagher et al., 2020).

The collection of articles in this Special Focus highlights the need to move trait-based ecology beyond the description of body size distributions. The simple reason for this is that the complexity of ecological communities is governed by multiple trait dimensions and by the interplay of traits across trophic levels (Fig. 1). Indeed, we can refine trait-based approaches by the identification, measurement and compilation of a new generation of animal functional traits, e.g., based on morphological, physiological or behavioural measurements. At first glance, this may stand in contrast to our call for identifying universal traits and general trait-based principles across the tree of life. It is undoubtedly true that a part of the future endeavour of trait-based ecology will require us to delve deep into the analysis of form-function relationships of specific groups of organisms. However, the knowledge gained by these analyses should provide insights and stimulation for the parallel efforts in many different animal taxa and ecosystems. If the promise of trait-based ecology is to provide the necessary means to generalize from one taxa to another and from one ecosystem type to another, we as functional ecologists must be ready to learn from the diversity of approaches in trait-based ecology. We hope that this Special Focus provides exactly this integrative perspective on recent trends in the analysis of animal functional traits and stimulates scientific progress towards a trait-based ecology for whole ecosystems.

References

Ali, J. R., Pigot, A. L., Blonder, B. W., & Tobias, J. A. (2023). Bird extinctions threaten to cause disproportionate reductions of functional diversity and uniqueness. *Functional Ecology*, *accepted*.

Bartomeus, I., Gravel, D., Tylianakis, J. M., Aizen, M. A., Dickie, I. A., & Bernard-Verdier, M. (2016). A common framework for identifying linkage rules across different types of interactions. *Functional Ecology*, *30*, 1894–1903. https://doi.org/10.1111/1365-2435.12666

Bascompte, J., García, M. B., Ortega, R., Rezende, E. L., & Pironon, S. (2019). Mutualistic interactions reshuffle the effects of climate change on plants across the tree of life. *Science Advances*, *5*, 1–9. https://doi.org/10.1126/sciadv.aav2539

Brose, U., Blanchard, J. L., Eklöf, A., Galiana, N., Hartvig, M., Hirt, M. R., Kalinkat, G., Nordström, M. C., O'gorman, E. J., Rall, B. C., Schneider, F. D., Thébault, E., & Jacob, U. (2017). Predicting the consequences of species loss using size-structured biodiversity approaches. *Biological Reviews*, *92*, 684–697. https://doi.org/10.1111/brv.12250

Brown, J. H., Hall, C. A. S., & Sibly, R. M. (2018). Equal fitness paradigm explained by a trade-off between generation time and energy production rate. *Nature Ecology and Evolution*, *2*, 262–268. https://doi.org/10.1038/s41559-017-0430-1

Capdevila, P., Beger, M., Blomberg, S. P., Hereu, B., Linares, C., & Salguero-Gómez, R. (2020). Longevity, body dimension and reproductive mode drive differences in aquatic versus terrestrial life-history strategies. *Functional Ecology*, *34*, 1613–1625. https://doi.org/10.1111/1365-2435.13604

Carlson, B. S., Rotics, S., Nathan, R., Wikelski, M., & Jetz, W. (2021). Individual environmental niches in mobile organisms. *Nature Communications*, *12*, 4572. https://doi.org/10.1038/s41467-021-24826-x

Carmona, C. P., Tamme, R., Pärtel, M., De Bello, F., Brosse, S., Capdevila, P., … Toussaint, A. (2021). Erosion of global functional diversity across the tree of life. *Science Advances*, *7*, eabf2675. https://doi.org/10.1126/sciadv.abf2675

Clavel, J., Julliard, R., & Devictor, V. (2011). Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and the Environment*, *9*, 222-228. https://doi.org/10.1890/080216

Colombo, G. T., Di Ponzio, R., Benchimol, M., Peres, C. A., & Bobrowiec, P. E. D. (2023). Functional diversity and trait filtering of insectivorous bats on forest islands created by an Amazonian mega dam. *Functional Ecology*, *online early*. https://doi.org/10.1111/1365-2435.14118

Crouch, N. M. A., & Jablonski, D. (2023). Is species richness mediated by functional and genetic divergence? A global analysis in birds. *Functional Ecology*, *online early*. https://doi.org/10.1111/1365-2435.14153

Dalsgaard, B., Maruyama, P. K., Sonne, J., Hansen, K., Zanata, T. B., Abrahamczyk, S., … Martín González, A. M. (2021). The influence of biogeographical and evolutionary histories on morphological trait-matching and resource specialization in mutualistic hummingbird–plant networks. *Functional Ecology*, *35*, 1120–1133. https://doi.org/10.1111/1365-2435.13784

Dehling, D. M., Bender, I. M. A., Blendinger, P. G., Böhning-Gaese, K., Muñoz, M. C., Neuschulz, E. L., … Stouffer, D. B. (2021). Specialists and generalists fulfil important and complementary functional roles in ecological processes. *Functional Ecology*, *35*, 1810–1821. https://doi.org/10.1111/1365-2435.13815

Dehling, D. M., & Stouffer, D. B. (2018). Bringing the Eltonian niche into functional diversity. *Oikos*, *127*, 1711–1723. https://doi.org/10.1111/oik.05415

Díaz, S., Purvis, A., Cornelissen, J. H. C., Mace, G. M., Donoghue, M. J., Ewers, R. M., Jordano, P., & Pearse, W. D. (2013). Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecology and Evolution*, *3*, 2958–2975. https://doi.org/10.1002/ece3.601

Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., … Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, *529*, 167–171. https://doi.org/10.1038/nature16489

Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., & Collen, B. (2014). Defaunation in the Anthropocene. *Science*, *345*, 401–406. https://doi.org/10.1126/science.1251817

Drag, L., Burner, R. C., Stephan, J. G., Birkemoe, T., Doerfler, I., Gossner, M. M., … Müller, J. (2023). High resolution 3D forest structure explains ecomorphological trait variation in assemblages of saproxylic beetles . *Functional Ecology, online early*. https://doi.org/10.1111/1365-2435.14188

Eisenhauer, N., Schielzeth, H., Barnes, A. D., Barry, K. E., Bonn, A., Brose, U., … Jochum, M. (2019). A multitrophic perspective on biodiversity–ecosystem functioning research. *Advances in Ecological Research*, *61*, 1–54. https://doi.org/10.1016/bs.aecr.2019.06.001

Enquist, B. J., Abraham, A. J., Harfoot, M. B. J., Malhi, Y., & Doughty, C. E. (2020). The megabiota are disproportionately important for biosphere functioning. *Nature Communications*, *11*, 699. https://doi.org/10.1038/s41467-020-14369-y

Etard, A., Morrill, S., & Newbold, T. (2020). Global gaps in trait data for terrestrial vertebrates. *Global Ecology and Biogeography*, *29*, 2143–2158. https://doi.org/10.1111/geb.13184

Ferrín, M., Márquez, L., Petersen, H., Salmon, S., Ponge, J. F., Arnedo, M., … Peguero, G. (2023). Trait-mediated responses to aridity and experimental drought by springtail communities across Europe. *Functional Ecology*, *online early*. https://doi.org/10.1111/1365-2435.14036

Fricke, E. C., Ordonez, A., Rogers, H. S., & Svenning, J. C. (2022). The effects of defaunation on plants' capacity to track climate change. *Science*, *375*, 210–214. https://doi.org/10.1126/science.abk3510

Funk, J. L., Larson, J. E., Ames, G. M., Butterfield, B. J., Cavender-Bares, J., Firn, J., … Wright, J. (2017). Revisiting the Holy Grail: Using plant functional traits to understand ecological processes. *Biological Reviews*, *92*, 1156–1173. https://doi.org/10.1111/brv.12275

Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., … Bommarco, R. (2015). Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proceedings of the Royal Society B: Biological Sciences*, *282*, 20142620. https://doi.org/10.1098/rspb.2014.2620

Gallagher, R. V., Falster, D. S., Maitner, B. S., Salguero-Gómez, R., Vandvik, V., Pearse, W. D., … Enquist, B. J. (2020). Open Science principles for accelerating trait-based science across the Tree of Life. *Nature Ecology and Evolution*, *4*, 294–303. https://doi.org/10.1038/s41559-020-1109-6

Gibb, H., Bishop, T. R., Leahy, L., Parr, C. L., Lessard, J. P., Sanders, N. J., … Wright, I. J. (2023). Ecological strategies of (pl)ants: Towards a world-wide worker economic spectrum for ants. *Functional Ecology*, *online early*. https://doi.org/10.1111/1365-2435.14135

Gravel, D., Albouy, C., & Thuiller, W. (2016). The meaning of functional trait composition of food webs for ecosystem functioning. *Philosophical Transactions of the Royal Society B*, *371*, 20150268. http://dx.doi.org/10.1098/rstb.2015.0268

Griffith, P., Lang, J. W., Turvey, S. T., & Gumbs, R. (2023). Using functional traits to identify conservation priorities for the world's crocodylians. *Functional Ecology*, *online early*. https://doi.org/10.1111/1365-

2435.14140

Grime, J. P. (1988). The CSR model of primary plant strategies–Origins, implications and tests. In L. D. Gottlieb & S. K. Jain (Eds.), Plant evolutionary biology (pp. 371–393). Springer. https://doi.org/10.1007/978-94-009-1207-6_14

Healy, K., Ezard, T. H. G., Jones, O. R., Salguero-Gómez, R., & Buckley, Y. M. (2019). Animal life history is shaped by the pace of life and the distribution of age-specific mortality and reproduction. *Nature Ecology and Evolution*, *3*, 1217–1224. https://doi.org/10.1038/s41559-019-0938-7

Herberstein, M. E., McLean, D. J., Lowe, E., Wolff, J. O., Khan, M. K., Smith, K., … Carthey, A. J. R. (2022). AnimalTraits - a curated animal trait database for body mass, metabolic rate and brain size. *Scientific Data*, *9*, 265. https://doi.org/10.1038/s41597-022-01364-9

Ibarra-Isassi, J., Handa, I. T., & Lessard, J. P. (2023). Community-wide trait adaptation, but not plasticity, explains ant community structure in extreme environments. *Functional Ecology*, *online early*. https://doi.org/10.1111/1365-2435.14185

Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., … Purvis, A. (2009). PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology*, *90*, 2648–2648. https://doi.org/10.1890/08-1494.1

Junker, R. R., Albrecht, J., Becker, M., Keuth, R., Farwig, N., & Schleuning, M. (2023). Towards an animal economics spectrum for ecosystem research. *Functional Ecology*, *online early*. https://doi.org/10.1111/1365-2435.14051

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., … Wirth, C. (2020). TRY plant trait database – enhanced coverage and open access. *Global Change Biology*, *26*, 119–188. https://doi.org/10.1111/gcb.14904

Kays, R., Davidson, S. C., Berger, M., Bohrer, G., Fiedler, W., Flack, A., Hirt, J., Hahn, C., Gauggel, D., Russell, B., Kölzsch, A., Lohr, A., Partecke, J., Quetting, M., Safi, K., Scharf, A., Schneider, G., Lang, I., Schaeuffelhut, F., … Wikelski, M. (2022). The Movebank system for studying global animal movement and demography. *Methods in Ecology and Evolution*, *13*, 419–431. https://doi.org/10.1111/2041-210X.13767

Kissling, W. D., Walls, R., Bowser, A., Jones, M. O., Kattge, J., Agosti, D., Amengual, J., Basset, A., Bodegom, P. M. Van, Cornelissen, J. H. C., Denny, E. G., Deudero, S., Egloff, W., Elmendorf, S. C., Navarro, L. M., Pawar, S., Pirzl, R., Rüger, N., & Sal, S. (2018). Towards global data products of Essential Biodiversity Variables on species traits. *Nature Ecology and Evolution*, *2*, 1531–1540. https://doi.org/10.1038/s41559-018-0667-3

Kraft, N. J. B., Valencia, R., & Ackerly, D. D. (2008). Functional traits and niche-based tree community assembly in an Amazonian forest. *Science*, *322*, 580–582. https://doi.org/10.1126/science.1160662

Lamanna, C., Blonder, B., Violle, C., Kraft, N. J. B., Sandel, B., Imova, I., … Enquist, B. J. (2014). Functional trait space and the latitudinal diversity gradient. *Proceedings of the National Academy of Sciences*, *111*, 13745–13750. https://doi.org/10.1073/pnas.1317722111

Laughlin, D. C. (2014). Applying trait-based models to achieve functional targets for theory-driven ecological restoration. *Ecology Letters*, *17*, 771–784. https://doi.org/10.1111/ele.12288

Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology*, *16*, 545–556. https://doi.org/10.1046/j.1365-2435.2002.00664.x

Lavorel, S., Storkey, J., Bardgett, R. D., de Bello, F., Berg, M. P., Le Roux, X., Moretti, M., Mulder, C., Pakeman, R. J., Díaz, S., & Harrington, R. (2013). A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. *Journal of Vegetation Science*, *24*, 942–948. https://doi.org/10.1111/jvs.12083

Maglianesi, M. A., Blüthgen, N., Böhning-Gaese, K., & Schleuning, M. (2014). Morphological traits determine specialization and resource use in plant-hummingbird networks in the Neotropics. *Ecology*, *95*, 3325–3334. https://doi.org/10.1890/13-2261.1

Marjakangas, E. L., Muñoz, G., Turney, S., Albrecht, J., Neuschulz, E. L., Schleuning, M., & Lessard, J. P. (2022). Trait-based inference of ecological network assembly: A conceptual framework and methodological toolbox. *Ecological Monographs, 92*, e1502. https://doi.org/10.1002/ecm.1502

Mason, N. W. H., De Bello, F., Doležal, J., & Lepš, J. (2011). Niche overlap reveals the effects of competition, disturbance and contrasting assembly processes in experimental grassland communities. *Journal of Ecology*, *99*, 788–796. https://doi.org/10.1111/j.1365-2745.2011.01801.x

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, *21*, 178–185. https://doi.org/10.1016/j.tree.2006.02.002

Neu, A., Cooksley, H., Esler, K. J., Pauw, A., Roets, F., Schurr, F. M., & Schleuning, M. (2023). Interactions between protea plants and their animal mutualists and antagonists are structured more by energetic than morphological trait matching. *Functional Ecology*, *online early*. https://doi.org/10.1111/1365-2435.14231

Palacio, F. X., Callaghan, C. T., Cardoso, P., Hudgins, E. J., Jarzyna, M. A., Ottaviani, G., … Mammola, S. (2022). A protocol for reproducible functional diversity analyses. *Ecography*, *2022*, e06287.

https://doi.org/10.1111/ecog.06287

Peña, R., Schleuning, M., Miñarro, M., & García, D. (2023). Variable relationships between trait diversity and avian ecological functions in agroecosystems. *Functional Ecology*, *online early*. https://doi.org/10.1111/1365-2435.14102

Pianka, E. R. (1970). On r-and K-selection. *The American Naturalist*, *104*, 592–597. https://doi.org/10.1086/282697

Pigot, A. L., Sheard, C., Miller, E. T., Bregman, T. P., Freeman, B. G., Roll, U., … Tobias, J. A. (2020). Macroevolutionary convergence connects morphological form to ecological function in birds. *Nature Ecology and Evolution*, *4*, 230–239. https://doi.org/10.1038/s41559-019-1070-4

Pincheira-Donoso, D. et al., (2023). Genome size does not influence extinction risk in the world's amphibians. *Functional Ecology*, *under review.* [ref. will be updated or removed in the final files]

Reich, P. B. (2014). The world-wide "fast-slow" plant economics spectrum: A traits manifesto. *Journal of Ecology*, *102*, 275–301. https://doi.org/10.1111/1365-2745.12211

Schleuning, M., Fründ, J., & García, D. (2015). Predicting ecosystem functions from biodiversity and mutualistic networks: An extension of trait-based concepts to plant-animal interactions. *Ecography*, *38*, 380–392. https://doi.org/10.1111/ecog.00983

Schleuning, M., Fründ, J., Schweiger, O., Welk, E., Albrecht, J., Albrecht, M., … Hof, C. (2016). Ecological networks are more sensitive to plant than to animal extinction under climate change. *Nature Communications*, 7, 13965. https://doi.org/10.1038/ncomms13965

Schmitz, O. J., Buchkowski, R. W., Burghardt, K. T., & Donihue, C. M. (2015). Functional Traits and Trait-Mediated Interactions: Connecting Community-Level Interactions with Ecosystem Functioning. *Advances in Ecological Research*, *52*, 319–343. https://doi.org/10.1016/bs.aecr.2015.01.003

Schneider, F. D., Fichtmueller, D., Gossner, M. M., Güntsch, A., Jochum, M., König-Ries, B., … Simons, N. K. (2019). Towards an ecological trait-data standard. *Methods in Ecology and Evolution*, *10*, 2006–2019. https://doi.org/10.1111/2041-210X.13288

Seibold, S., Cadotte, M. W., MacIvor, J. S., Thorn, S., & Müller, J. (2018). The Necessity of Multitrophic Approaches in Community Ecology. *Trends in Ecology & Evolution*, *33*, 754–764. https://doi.org/10.1111/cobi.12427

Srivastava, D. S., MacDonald, A. A. M., Pillar, V. D., Kratina, P., Debastiani, V. J., Guzman, L. M., Trzcinski, M. K., Dézerald, O., Barberis, I. M., de Omena, P. M., Romero, G. Q., Ospina-Bautista, F., Marino, N. A. C., Leroy, C., Farjalla, V. F., Richardson, B. A., Gonçalves, A. Z., Corbara, B., Petermann, J. S., … Céréghino, R. (2023). Geographical variation in the trait-based assembly patterns of multitrophic invertebrate communities. *Functional Ecology*, *online early*. https://doi.org/10.1111/1365-2435.14096

Stearns, S. C. (1976). Life-history tactics: A review of the ideas. *The Quarterly Review of Biology*, *51*, 3–47. https://doi.org/10.1086/409052

Stouffer, D. B., Rezende, E. L., & Amaral, L. A. N. (2011). The role of body mass in diet contiguity and food-web structure. *Journal of Animal Ecology*, *80*, 632–639. https://doi.org/10.1111/j.1365-2656.2011.01812.x

Suding, K. N., Lavorel, S., Chapin III, F. S., Cornelissen, J. H. C., Díaz, S., Garnier, E., … Navas, M.-L. (2008). Scaling environmental change through the framework for plants. *Global Change Biology*, *14*, 1125–1140. https://doi.org/10.1111/j.1365-2486.2008.01557.x

Tobias, J. A., Sheard, C., Pigot, A. L., Devenish, A. J. M., Yang, J., Sayol, F., … Schleuning, M. (2022). AVONET: morphological, ecological and geographical data for all birds. *Ecology Letters*, *25*, 581–597. https://doi.org/10.1111/ele.13898

Villéger, S., Mason, N. W. H., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, *89*, 2290–2301. https://doi.org/10.1890/07-1206.1

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, *116*, 882–892. https://doi.org/10.1111/j.2007.0030-1299.15559.x

Violle, C., Reich, P. B., Pacala, S. W., Enquist, B. J., & Kattge, J. (2014). The emergence and promise of functional biogeography. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 13690–13696. https://doi.org/10.1073/pnas.1415442111

Walter, H. E., Pagel, J., Cooksley, H., Neu, A., Schleuning, M., & Schurr, F. M. (2023). Effects of biotic interactions on plant fecundity depend on spatial and functional structure of communities and time since disturbance. *Journal of Ecology*, *online early*. https://doi.org/10.1111/1365-2745.14018

Williamson, J., Teh, E., Jucker, T., Brindle, M., Bush, E., Chung, A. Y. C., … Slade, E. M. (2022). Local-scale temperature gradients driven by human disturbance shape the physiological and morphological traits of dung beetle communities in a Bornean oil palm–forest mosaic. *Functional Ecology*, *36*, 1655–1667. https://doi.org/10.1111/1365-2435.14062

Wilman, H., Belmaker, J., Simpson, J., de La Rosa, C., Rivadeneira, M. M., & Jetz, W. (2014). EltonTraits 1.0 : Species-level foraging attributes of the world’s birds and mammals. *Ecology*, *95*, 2027. https://doi.org/10.1890/13-1917.1

Wootton, K. L., Curtsdotter, A., Roslin, T., Bommarco, R., & Jonsson, T. (2023). Towards a modular theory of trophic interactions. *Functional Ecology*, *online early*. https://doi.org/10.1111/1365-2435.13954

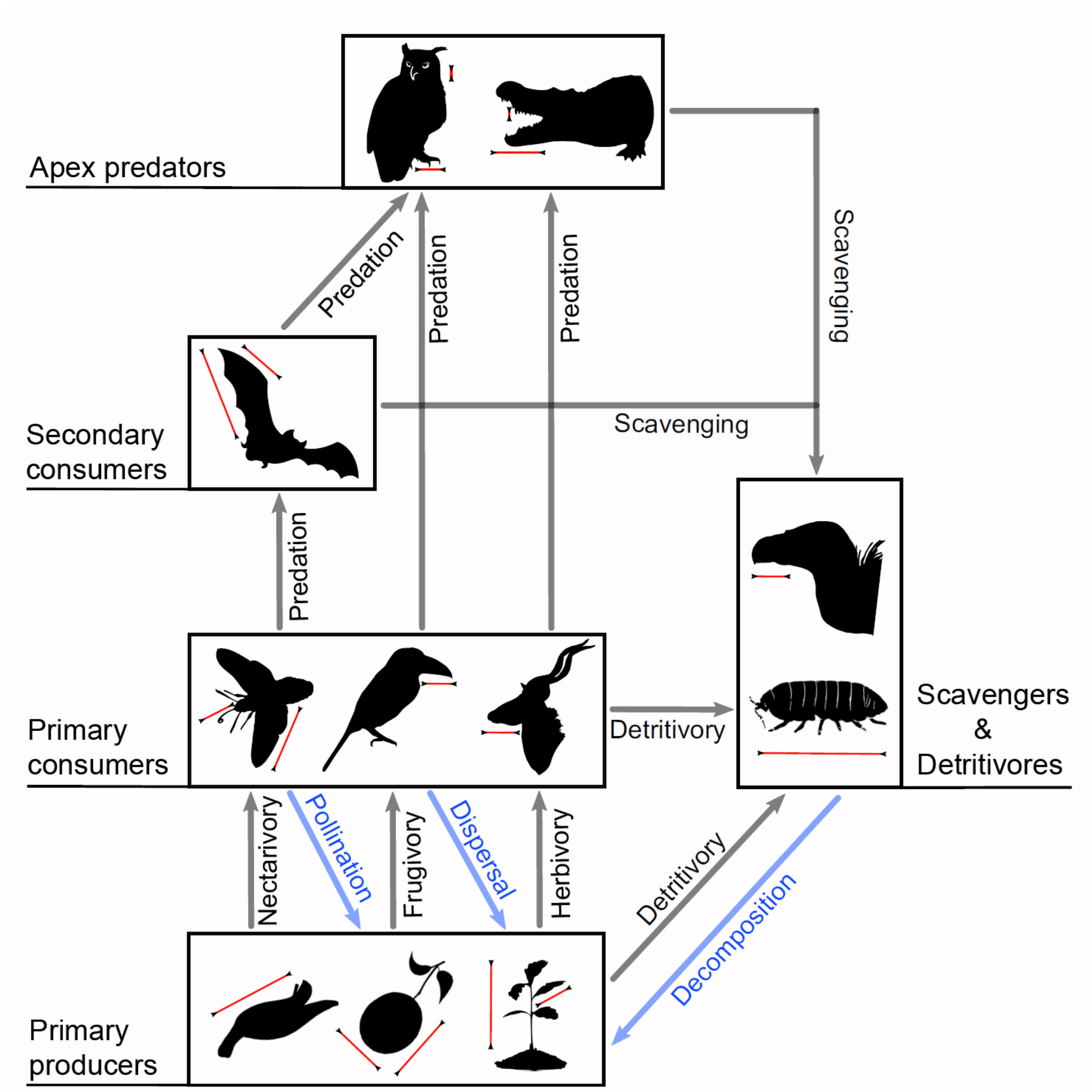

Figure 1. Functional traits across trophic levels. A conceptual diagram showing a simplified ecosystem with plants (primary producers) at the lowest trophic level and animals occupying higher trophic levels. Selected functional traits are indicated by red measurement bars, and the links between traits across trophic levels are shown by grey arrows. These traits primarily mediate trophic interactions between organisms located at different trophic levels, e.g., via trait matching between flowers and fruits and their interacting animal partners. The same traits also influence interactions within trophic levels, e.g., via competitive interactions between nectarivores or frugivores feeding on the same type of plant resources. The shown traits further mediate feedback effects onto lower trophic levels and shape important ecosystem functions such as pollination and seed dispersal (blue arrows and font).