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Cover image: A Crimson Topaz (*Topaza pella*) alights on the flamboyant blooms of a tulip tree (*Spathodea campanulata*) to feed on nectar (credit: Joe Tobias). This image encapsulates the vision for trait-based ecology set out by M. Schleuning et al. (doi:10.1111/1365-2435.14246) in their editorial to this Special Focus on animal functional traits. Until recently, plants have taken centre stage in driving the rapid progress of trait-based ecology, but the conclusions are mostly limited in relevance to the primary producers in ecosystems and largely ignore their interactions with various types of consumers, such as herbivores, pollinators and seed-dispersers. The focus is currently expanding outward – and upward! – to include the traits of animals operating at these higher trophic levels, opening up new fields of investigation into ecological processes relevant to entire food-webs. The beak of the Crimson Topaz, for example, is characteristic of avian pollinators and conveys information about the types of flowers visited by this hummingbird. The articles contained in this Special Focus showcase a collection of studies on animals ranging in size from tiny invertebrates to crocodiles, offering insights into the path forward for trait-based analyses of whole ecosystems.

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GUEST EDITORIAL

Animal Functional Traits

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), Frankfurt (Main), Germany

[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, UK

Correspondence
Matthias Schleuning
Email: matthias.schleuning@senckenberg.de

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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, and an over-reliance on plant traits therefore neglects the complexity and importance of biotic interactions across trophic levels.
2. The need to expand the focus of trait-based ecology to account for trophic complexity 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 animal taxa has opened up new possibilities for testing ecological theory.
3. In this Special Focus, we explore how trait-based ecology can expand the scope of investigation from single to multiple trophic levels, how insights from these investigations can be used to upscale understanding from local communities to biogeographical 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, particularly of the mechanisms underpinning large-scale biodiversity patterns. Furthermore, 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, competition, ecological networks, ecosystem functioning, food webs, macroecology, species coexistence, trophic interactions

1 | INTRODUCTION

Ecological research addresses the fundamental question of how organisms interact with their environment and with other organisms (McGill et al., 2006). The identification of processes underpinning these interactions is a key step forward from the description of ecological processes towards a more mechanistic understanding that can form the basis for predictions (Funk et al., 2017). One of the most promising ways to reveal underlying mechanisms involves the analysis of ecological communities with species traits (McGill et al., 2006; Violle et al., 2007). Over recent 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 largely within a single trophic level (Kraft et al., 2008; Mason et al., 2011). Consequently, 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, global-scale 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). These traits determine how organisms respond to their abiotic and biotic environment and how they contribute to ecological processes and ecosystem functions (Suding et al., 2008). The power of functional traits to generalize ecological understanding from single taxa to entire communities has driven rapid progress in ecological research over the last two decades (Funk et al., 2017; Lavorel & Garnier, 2002), leading to the identification of core principles in community ecology and ecosystem science. For instance, studies of plants 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), thereby structuring variation in plant form and function at the global scale (Díaz et al., 2016).

Trait-based concepts have also taken root in the field of ecosystem science. For example, 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). Clearly, plants can teach us a great deal about the fundamental properties of biodiversity, yet trait-based approaches will only reflect the full complexity of ecosystems if they are designed to account for the biotic interrelationships across trophic levels (Figure 1).

One way that traits can shed light on trophic complexity is through the formulation of interaction rules between species located at different trophic levels. 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 (Brose et al., 2017; Stouffer et al., 2011). 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 on lower trophic levels through ecosystem functions such as pollination, seed dispersal and decomposition (Figure 1). Trait-matching frameworks have mostly been derived from the analysis of ecological networks (Bartomeus et al., 2016; Schleuning et al., 2015), echoing earlier concepts derived primarily 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; Tobias, 2022). Given this upsurge of data, trait-based approaches have the potential to be a game-changer in ecosystem science offering new mechanistic insights into the form and function of ecological communities and networks. 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 is well studied, such as plants (Díaz et al., 2016) and birds (Pigot et al., 2020). The capacity of trait-based approaches to generalize

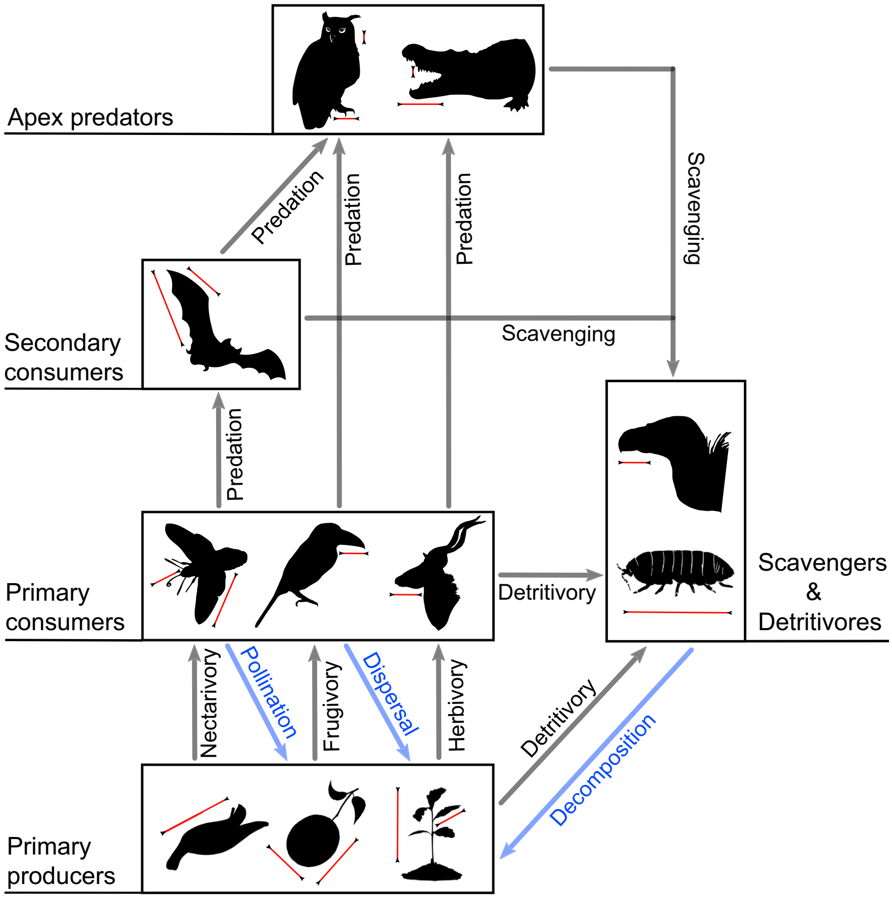

FIGURE 1 Functional traits mediate interactions between organisms across all trophic levels. A combination of plant and animal traits is therefore required to address the trophic complexity of ecosystems. This conceptual diagram shows a simplified ecological network with plants (primary producers) at the lowest trophic level and animals occupying higher trophic levels. Selected traits are indicated by red measurement bars, and the links between traits across trophic levels are shown by grey arrows. Examples of trait-mediated interactions between organisms located at different trophic levels include trait matching between flowers and fruits and their interacting animal partners. The same traits also influence interactions within trophic levels, for example, via competitive interactions between plant or animal species with similar ecological niches. Crucially, traits mediate reciprocal feedback effects between trophic levels, with resource uptake by consumers delivering ecological services to producers, such as pollination and seed dispersal (blue arrows and font). Silhouettes were obtained from phylopic.org and vecteezy.com

ecological understanding across trophic levels and spatial scales therefore remains to be tested for most animal taxa and ecosystems.

2 | KEY QUESTIONS OF THE SPECIAL FOCUS

With this Special Focus, we draw together different strands of research on animal functional traits and associated concepts. We aim to cover the broadest possible range of animal taxa to gauge the current state-of-the-art and to address three prominent questions in 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 biogeographical 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.

3 | 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 from tiny springtails to huge crocodiles, spanning a range of body mass from about 0.1 mg to 1000 kg, and inhabiting terrestrial and aquatic ecosystems. The featured animal taxa are located at different trophic levels including primary consumers, secondary consumers, apex predators and detritivores (Figure 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 a 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. Different functional traits may shape species interactions within and across trophic levels (Walter et al., 2023), demonstrating that multiple traits jointly structure multi-trophic communities and their respective ecosystem functions (Gravel et al., 2016). In particular, morphological traits alone may not always be sufficient for predicting trophic interactions and functions (Bartomeus et al., 2016). Indeed, 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 evident in dung beetle 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 about their environmental preferences compared to an integrative ecological classification of species (Drag et al., 2023), although whether this is because the relevant morphological traits remained unmeasured is difficult to determine. This demonstrates that, as functional ecologists, we need to continue the quest for the most informative traits. Only by identifying, measuring and analysing more of these traits, will we be able to fully capitalize on the potential of trait-based ecology and uncover the fundamental processes operating within and across trophic levels.

4 | QUESTION 2. UPSCALING UNDERSTANDING FROM SMALL TO LARGE SPATIAL SCALES

Ecologists and biogeographers strive to generalize understanding from one ecosystem to another and from small to large spatial scales using functional traits (Violle et al., 2014). The accurate identification of such generalities requires the availability of global trait datasets, ideally with a high level of species coverage (Tobias, 2022). Recent progress in the availability of global trait datasets (Griffith et al., 2023; Pincheira-Donoso et al., 2023; Tobias et al., 2022) provides the basis for testing long-standing questions on global biodiversity patterns with trait-based approaches. 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 biogeographical 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 terrain of functional biogeography are promising (Violle et al., 2014) and call for intensified efforts in the compilation of comprehensive global trait data for many more taxonomic groups (Gallagher et al., 2020; Tobias, 2022). It will be exciting to see how these ongoing efforts will further advance understanding of the mechanisms underlying global biodiversity patterns.

5 | QUESTION 3. PREDICTING THE ECOSYSTEM-LEVEL CONSEQUENCES OF BIODIVERSITY LOSS

One of the most alluring promises of trait-based ecology is to generalize 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 species-level to ecosystem-level understanding can now principally be 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). In amphibians, extinction risk was related to a large body size across 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). 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 projected species extinctions may cause shifts in size-independent trait dimensions such as those related to climatic tolerance, movement and trophic interactions, with potentially important consequences for ecosystem functioning (Ali et al., 2023; Griffith et al., 2023). Although 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), only few studies have empirically tested how such changes affect 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 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), thereby providing a basis for predicting the consequences of biodiversity loss for whole ecosystems.

6 | 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 providing preliminary answers. The wider potential of trait-based ecology emerges from its power to synthesize scientific insight 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 a functional perspective to conservation biology and ecosystem science (Laughlin, 2014). From a multi-trophic perspective, we have only just begun to address these goals and, despite decades of trait-based ecology, have achieved a fragmentary knowledge biased towards specific taxa and biogeographical regions (Etard et al., 2020). We therefore argue that the future of trait-based ecology lies in the expansion and integration of trait data, concepts and knowledge across taxonomic and biogeographical realms.

The asymmetric advances in trait data collection have led to an uneven availability of data across taxa. Plant ecologists were quick to identify the rich 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; Tobias, 2022). This process of integrating 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). The emerging 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 border between plant and animal kingdoms. Instead, it provides ready-to-use pathways for comparative analyses based on universal functional traits applicable to both plants and animals, and fundamental to their interactions and codependencies (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 until recently focused on traits that are relatively easy to measure and which vary mostly at species rather than individual level (Herberstein et al., 2022; Tobias et al., 2022). Traits related to phenotypic plasticity and animal behaviour often define responses of individual animals to global change (Carlson et al., 2021). Yet, these traits are underrepresented in global datasets, despite the increasing availability of such data, for example, on avian phenology (Bailey et al., 2022) or animal movements (Kays et al., 2022). Trait-based ecology therefore needs to develop unifying frameworks that are able to integrate trait data describing individual-level and species-level variation in 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 timely opportunities, the research community is increasingly aware of the need for trait data integration coupled with the development of interoperable methods and data protocols (Palacio et al., 2022; Schneider et al., 2019).

The collection of articles in this Special Focus highlights the need to move trait-based ecology far 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 (Figure 1). Indeed, we can refine trait-based approaches by the identification, measurement and compilation of a new generation of animal functional traits based on morphological, physiological or behavioural measurements. This expansion of focus is a necessary accompaniment to our call for identifying universal traits and general trait-based principles across the tree of life. Overall, the future success of trait-based ecology will require us to delve deep into the analysis of form–function relationships of many (more) groups of organisms. Not only is this endeavour likely to be fruitful, it should provide stimulation for ongoing research in many different animal taxa and ecosystems. If the promise of trait-based ecology to generalize understanding from one taxa to another is to be fully realized, 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 an integrative perspective on recent trends in the analysis of animal functional traits and stimulates scientific progress towards a trait-based ecology for whole ecosystems.

AUTHOR CONTRIBUTIONS

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

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CONFLICT OF INTEREST

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No data were used for this Editorial.

ORCID

Matthias Schleuning https://orcid.org/0000-0001-9426-045X
Daniel García https://orcid.org/0000-0002-7334-7836
Joseph A. Tobias https://orcid.org/0000-0003-2429-6179

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