Trends in Ecology & Evolution

CellPress

Review

Functional Rarity: The Ecology of Outliers

Cyrille Violle,[1,*] Wilfried Thuiller,[2] Nicolas Mouquet,[3,4] François Munoz,[5,6] Nathan J.B. Kraft,[7] Marc W. Cadotte,[8,9] Stuart W. Livingstone,[10] and David Mouillot[4,11]

Rarity has been a central topic for conservation and evolutionary biologists aiming to determine the species characteristics that cause extinction risk. More recently, beyond the rarity of species, the rarity of functions or functional traits, called functional rarity, has gained momentum in helping to understand the impact of biodiversity decline on ecosystem functioning. However, a conceptual framework for defining and quantifying functional rarity is still lacking. We introduce 12 different forms of functional rarity along gradients of species scarcity and trait distinctiveness. We then highlight the potential key role of functional rarity in the long-term and large-scale maintenance of ecosystem processes, as well as the necessary linkage between functional and evolutionary rarity.

Trends

A framework for the definition and quantification of functional rarity is missing.

We define functional rarity using both species sparseness and trait distinctiveness.

We introduce 12 different forms of functional rarity.

We discuss the effect of each form of functional rarity on ecosystem function.

The necessary linkage between functional and evolutionary rarity is highlighted.

The Multiple Facets of Rarity

Rarity has fascinated ecologists and evolutionary biologists [1], and has become the cornerstone of many research fields, and especially of conservation biology [2–4]. Why do species become rare? Why are there so many rare species on Earth? Many studies have examined the biological characteristics of species with a view to explaining the reasons for their rarity (e.g., [5–9]) and the potential consequences of their extirpation [3,4]. Rare species perform different functions in ecosystems, some being redundant with those of many other rare and common species, while others are unique [10–13]. Surprisingly, few studies have investigated the rarity of functions (hereafter **functional rarity**; see Glossary) within communities and its importance for the functioning of ecosystems [12,14,15].

While human societies have often placed higher value on rare versus common ones, rarity and commonness remain generic and vague concepts. Indeed, some species can be commonly found at a large geographic scale while being locally rare within communities, such as apex predators. Others can be commonly found within communities but possess unique traits or genes. These examples point out that rarity and commonness have multiple facets [16,17]. Therefore, in the same way as definitions and estimates of biodiversity have been recently expanded to include spatial, phylogenetic, and functional dimensions [18–20], our definitions of rarity and commonness need to be revised in a broader quantitative framework that captures additional dimensions of biodiversity. The seminal paper of Rabinowitz [21] provided the foundation for such a framework that included seven forms of rarity based on three species characteristics: geographic range, habitat specificity, and local abundance. This typology of rarity is able to take into account the main aspects related to the spatial distribution of species, but it remains silent on species' functions. Given the increasingly important role of functional diversity in community ecology, biogeography, and conservation biology [22–26], there is an urgent need to develop a framework of functional rarity and associated metrics that directly combine **functional trait** information and species abundances across scales.

[1]Centre d'Ecologie Fonctionnelle et Evolutive (CEFE), Unité Mixte de Recherche (UMR) 5175, Centre National de la Recherche Scientifique (CNRS), Université de Montpellier, Université Paul-Valéry Montpellier, Ecole Pratique des Hautes Etudes (EPHE), Montpellier, France
[2]Université Grenoble Alpes, CNRS, LECA (Laboratoire d'Ecologie Alpine), F-38000 Grenoble, France
[3]CNRS UMR 5554, Institut des Sciences de l'Evolution, Université de Montpellier 2, Montpellier, France
[4]Marine Biodiversity, Exploitation, and Conservation (MARBEC), UMR 9190 Institut de Recherche pour le Développement (IRD)–CNRS–Université de Montpellier (UM)–Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER), Université Montpellier, Montpellier , France
[5]Université de Montpellier, botAnique et Modélisation de l'Architecture des Plantes et des végétations (AMAP), Montpellier CEDEX 5, France

Better characterizing functional rarity goes beyond the issue of the mere understanding of why species are rare or common; it can also be key to better understanding the relationship between biodiversity and ecosystem functioning (BEF). Growing consensus suggests that BEF relationships are driven by the diversity of functions carried out by species and their individuals within an ecosystem [27–29]. In parallel, the disproportionate effect of some rare species (e.g., keystone species) on ecosystem processes is increasingly reported [12,15,30]. This calls for a deeper integration of functional rarity in BEF studies, particularly to meet the challenge of maintaining multiple processes under global changes [31].

In this paper we propose a conceptual framework that builds on the classification of Rabinowitz to define and quantify functional rarity. For this we identify four cross-species scarcity–trait distinctiveness dichotomies and two geographic rarity categories (restricted vs widespread species), leading to 12 different forms of functional rarity. Next, we discuss the potential effect of each form of functional rarity on the functioning of ecosystems. As a perspective, we propose future directions, including the necessary linkage between functional and evolutionary rarity, which constitute an important avenue for both BEF research and conservation biology.

[6]French Institute of Pondicherry, Pondicherry 605001, India
[7]Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095, USA
[8]Department of Biological Sciences, University of Toronto Scarborough, Toronto, ON, Canada
[9]Ecology and Evolutionary Biology, University of Toronto, Toronto, ON, Canada
[10]Department of Physical and Environmental Science, University of Toronto Scarborough, Toronto, ON, Canada
[11]Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD, Australia

*Correspondence:
cyrille.violle@cefe.cnrs.fr (C. Violle).

On the Importance of Functional Rarity

The maintenance of scarce and unique phenotypes in communities is a well-known phenomenon because lower frequency and greater distinctiveness limit both intra- and interspecific competition (negative frequency-dependence) [32]. It has also been described as a 'strategy' for a species to expand its niche width via a release of intraspecific competition or the exploitation of alternative resources [33]. In addition, both microbial experiments and theoretical studies have emphasized the positive role of rare phenotypes in the rescue of ecological communities in face of severe environmental stresses [34,35]. However this principle has not been tested over large scales where functional rarity needs to be well defined and assessed.

There is contrasting evidence about the importance of rare species for ecosystem functioning [13,36]. An intuitive line of reasoning assumes that rare species have very little impact on ecosystems according to the 'mass ratio hypothesis' [37]. This common belief lies in the long tradition of using total biomass or productivity as a proxy for ecosystem functioning, where dominant species have strong effects while rare species have marginal influence. However, the need to deal with ecosystem multifunctionality, resilience or resistance across time, and disturbances or dependence upon some keystone species challenges this simplistic view [13,30]. For instance, even at low abundance, predators can have disproportionate impacts on ecosystem functioning through top-down control along the trophic chain and the associated energy fluxes. Because predators are often among the most endangered [38,39], their loss will likely have strong effects on ecosystems. A good example is given by the giant moray eel (*Gymnothorax javanicus*) that hunts at night within the labyrinth of coral reefs. This species possesses distinct functional characteristics (elongated shape and strong olfactory capacities), and has no equivalent in its ability to prey on hard-to-access dead or weak animals, thus accelerating nutrient cycling in oligotrophic ecosystems [40]. The influence that the giant moray eel has on ecosystem functioning appears irreplaceable, as suggested by its very unique combination of traits. Despite the potential importance of functional rarity on ecosystem functioning, only a handful of studies in the literature address this issue [10,12,40]. This is certainly due in part to that lack of a framework for estimating functional rarity across scales.

We propose here an **ecology of outliers** dedicated to understanding better (i) how to define and identify those outliers given their local or regional abundances and trait distinctiveness, (ii) the consequences of the persistence of those outliers for the structure and dynamics of communities and ecosystems, and (iii) the distribution of these outliers across the tree of life.

Functional Rarity: A Conceptual Framework

The definition of functional rarity is the most crucial conceptual point before making significant progress in this new ecology of outliers.

For decades ecological rarity has been estimated at the species level using three main characteristics ultimately related to extinction risk [41]: geographical range, habitat specificity, and local abundance. The combination of these three characteristics defines seven forms of species rarity [21], with the rarest species having small range, a high level of habitat specificity, and locally low abundance. Our proposed facets of functional rarity are partly based on these basic forms (for instance local abundance in Figure I of Box 1). Complementing this, quantifying functional rarity must include the extent to which species traits, used as proxies to represent functions, trophic links, and niche axes [42–47], are more or less distinct or redundant within local communities or larger-scale species assemblages [40,48,49] (Box 1).

Using a set of dichotomies for species characteristics related to their frequencies and their traits, we propose to introduce the different facets of functional rarity. For the distribution of species we follow the steps of Rabinowitz [21] with two levels of rarity across scales. At the local scale (e.g., at the community scale) we discriminate scarce versus abundant species, while at the regional level we define restricted versus widespread species (Table 1). In the same vein, we propose to differentiate the rarity versus commonness of species traits compared to a given pool at the local and the regional levels. At the local scale we choose to define functionally distinct species as those having traits dissimilar from those of other species, and functionally redundant species as those having the traits that are most abundant at local scale. At the regional scale a dichotomy can be made between species possessing unique traits, in other words traits that are not shared by any other species in the pool, and species possessing shared traits. Based on these four crossed dichotomies we can define 16 potential forms of functional rarity. Of these 16, four are never met because species cannot be functionally redundant at the local scale while being unique at the regional scale (Table 1). We therefore end

Box 1. From the Rarity of Species to the Rarity of Functions

As the use of functional traits rapidly expands, the question of which traits, or combinations of traits, can be the most informative is crucial because particular traits may reveal different information about the functional distinctiveness of a species. Moreover, if the selected traits are highly correlated with each other, then the 'true' functional distinctiveness, which may become evident if other traits or combinations of traits were considered, can be obscured. It is also important to note that, although trait databases have emerged in many different kingdoms [83–86], they are often biased towards traits measured on common species [87–89], and this can impede an accurate assessment of functional distinctiveness.

When selecting and analyzing functional trait information for the identification of functionally distinct species, researchers would do best to identify traits which can have implications for multiple ecological functions [29]. Given this complexity, three main approaches have emerged. The first is to use a few traits where the functional consequences are well understood. If the ecological consequences of traits are ambiguous, a second approach is to use a multitude of traits as a way to capture overall ecological distinctiveness. The third approach is a hybrid option, where well-understood traits are either analyzed separately or are combined with ambiguous traits to assess how trait inclusion alters the interpretation of functional distinctiveness.

Once traits have been selected for the whole set of species, the functional distances between all pairs of species can be quantified (Figure I). Several metrics are classically used depending on trait categories and potential missing values [58,59]. The functional distinctiveness of a given species can then be assessed using its functional distance to the rest of the community (Box 2).

The last step is to combine species rarity, for instance based on local abundance (Figure I), and trait distinctiveness into an index of functional rarity: the functionally rarest species have low abundance and the most distinct traits (species A in Figure I), while the functionally commonest species are those with highest abundances and the least distinct traits (species C in Figure I).

Glossary

Ecology of outliers: a research area that studies how and why species (or organisms) are outliers given their local or regional abundances and trait distinctiveness, and the consequences of the persistence of those outliers for the structure and dynamics of communities and ecosystems.

Functional distinctiveness (or trait distinctiveness): local-scale characteristics of a species (or an organism) having traits dissimilar from those of other species (organisms) in the community. A metric of functional distinctiveness assesses whether a species (or an organism) is more or less functionally close to the rest of the community.

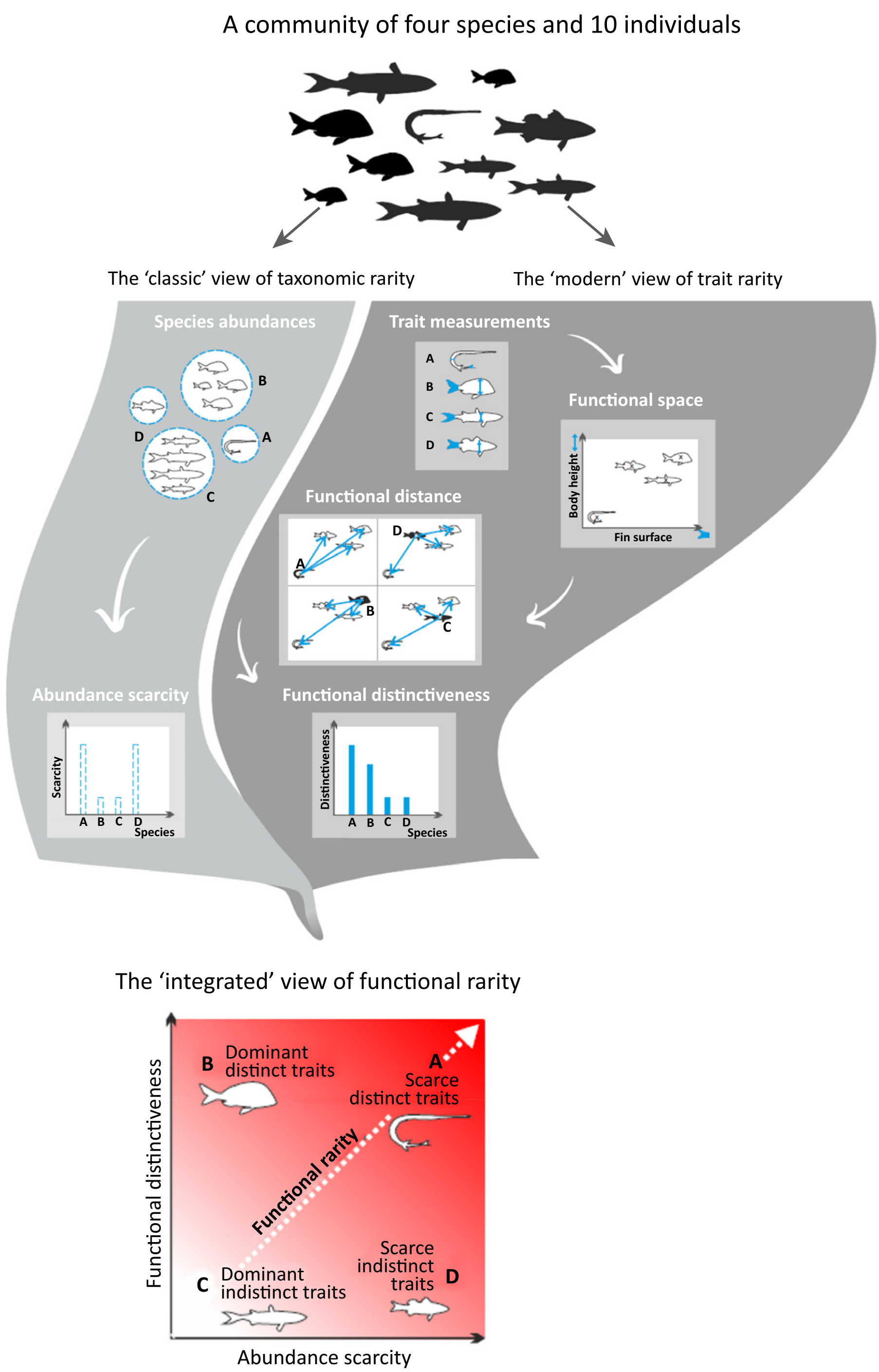
Functional rarity (or trait rarity): feature of a species (or an organism) that integrates both functional distinctiveness and taxonomic scarcity at the local scale, or both functional uniqueness and taxonomic restrictedness at the regional scale. Functionally rare species are ecological outliers. They possess the highest functional rarity value in the community (local scale) or in the regional pool (regional scale).

Functional trait: any fitness-related morphological, physiological, phenological or behavioral feature measurable at the individual level.

Functional uniqueness (or trait uniqueness): regional-scale feature of a species (or an organism) possessing unique traits, in other words traits that are not shared by any other species in the regional pool. A metric of functional uniqueness assesses the extent to which a species (or an organism) has no functional equivalent in the regional pool.

Taxonomic restrictedness (or species restrictedness): regional-scale characteristics of a species being geographically restricted (e.g., small extent of occurrence or small area of occupancy).

Taxonomic scarcity (or species scarcity): local-scale feature of a species with low relative abundance (in terms of number of individuals or biomass) in the community.



Trends in Ecology & Evolution

Figure I. Functional Rarity Types in Local Communities Are Assessed in Both Abundance and Trait Space by Combining the Classical View of Taxonomic Rarity and the Modern View of Trait Rarity. Using a 10-individual community of four species, we highlight different facets of functional rarity integrated into a single framework. The four species correspond to archetypal situations at the extremes of the abundance scarcity and functional distinctiveness gradients, species A being the ecological outlier (highest functional rarity value) in the community, while species C is the ecological norm (lowest functional rarity value).

Table 1. The 12 Forms of Functional Rarity

			Species frequency			
			Geographically restricted		Geographically widespread	
			Locally scarce	Locally abundant	Locally scarce	Locally abundant
Species traits	Geographically unique	Locally distinct	Rare traits irrespective of the scale and the species pool	Specialized traits supported by few species	Widespread traits supported by few scarce species	Traits supported by few common species
		Locally redundant	**Impossible**	**Impossible**	**Impossible**	**Impossible**
	Geographically shared	Locally distinct	Traits supported by many rare species that do not co-occur	Specialized traits supported by many species	Traits supported by many widespread but locally sparse species that do not co-occur	Traits supported by many common species that do not co-occur
		Locally redundant	Traits supported by many rare species	Specialized traits supported by many species	Traits supported by many widespread but locally sparse species	Common traits irrespective of the scale and the species pool

up with 12 potential forms of functional rarity among which we identify two extremes: rare traits, exhibited by a few scarce, range-restricted species, and common traits, supported by many widespread and locally abundant species.

At each spatial scale we can also visualize functional rarity versus commonness with a biplot based on relative species frequencies and trait differences (illustrated at the local scale in Figure I of Box 1). Category A corresponds to rare traits while category C is for common traits in a community. Because scarce species and redundant traits tend to be the most frequent within communities [40], we expect to find a majority of species belonging to category D, whereas species from category B, in other words those dominating communities and possessing distinct traits, may be the least frequent [17,50]. Given the heterogeneous distribution of species richness among these categories, we suggest defining the bounds of each category with quantile values. To better discriminate rare versus common traits, an alternative is to use the 5% most-extreme values as a cut-off.

Although this framework is focused on defining functional rarity at the species level, it can be easily applied to a variety of taxonomic and population-level scales. For example, the recent awareness that intraspecific functional variability can have important impacts not only on local adaptation but also on community assembly and ecosystem functioning [51–53] has led to increased measurement of traits of individuals within species at different locations [54], as well as the development of new diversity metrics [55,56]. Our framework can be easily extended to include intraspecific variability because functional rarity can be calculated at the individual level [48]. This can also be further extended to include lower levels of integration such as genotypes, genes, or transcriptomes.

Measuring Functional Rarity

For over three decades a myriad of metrics have been developed to quantify many facets of biodiversity [57–63]. However, this prolific field has poorly integrated the measurement of functional rarity versus commonness.

To combine the different facets of rarity (Table 1 and Box 1) into a single index, we propose an 'integrated' view of functional rarity that accounts for both the **functional distinctiveness**/uniqueness of a species (based on traits, Box 2) and its **taxonomic scarcity/restrictedness** (based on local and regional frequencies, Box 3). The functional rarity (*FR*) of species *i* can be expressed at the local scale as:

$$FR_i = f(D_i, S_i)$$

Box 2. Measuring Functional Distinctiveness and Uniqueness

The main difference between functional distinctiveness and uniqueness is the scale at which the rarity of species traits is assessed. At the local scale, functional distinctiveness takes into account all species within the community to measure whether species *i* is more or less functionally close to the rest of the community [40]. At the regional scale, functional uniqueness relies on the functionally nearest species to measure the extent to which species *i* has no functional equivalent (or redundancy) in the pool [90]. These two indices simply correspond to the mean pairwise distance (MPD) and the mean nearest taxon distance (MNTD) that measure the isolation (based on phylogenetic relationships) of each species from all the others and to its closest relative, respectively [91].

The functional distinctiveness *D* of species *i* is thus defined as the mean functional distance to the *N* other species:

$$D_i = \frac{\sum_{j=1, j \neq i^*}^{N} d_{ij}}{N - 1} \quad \text{(Equation I)}$$

where *N* is the number of species within the community and d_{ij} is the functional distance between species *i* and *j*. d_{ij} is scaled between 0 and 1 by dividing all functional distances between species by the maximum value among pairs within the community.

Functional distinctiveness *D* can also be weighted by species relative abundance *Ab* because a species is even more distinct if it does not share traits with the most abundant species within the community:

$$D_i = \frac{\sum_{j=1, j \neq i}^{N} d_{ij} \times Ab_j}{\sum_{j=1, j \neq i^*}^{N} Ab_j} \quad \text{(Equation II)}$$

To avoid considering the abundance of focal species *i* in the calculation of functional distinctiveness, because it is already acknowledged to assess its local scarcity (Box 3), Ab_j is the relative abundance of species *j* among the $N-1$ remaining species.

D_i is low when species *i* is functionally close to many others and/or to the most-dominant species within the community (high Ab_j values). As an extreme case D_i tends to 0 when a species is hyper-dominant (Ab_i tends to 1, and the others to 0) and/or when all species are redundant with species *i* (d_{ij} tends to 0). At the opposite extreme D_i tends to 1 when the most-distant species *j* (d_{ij} = 1) is hyper-dominant (Ab_j tends to 1), or when all species have the maximum distance to species *i* within the community. D_i thus ranges between 0 and 1.

Functional uniqueness (U_i) is measured by the functional distance to the nearest neighbor (or to the *k* nearest neighbors) within the regional species pool as:

$$U_i = \min(d_{ij}) j = i* \quad \text{(Equation III)}$$

U_i is high when species *i* has a unique combination of traits compared to other species and more particularly has a high functional distance even with its closest species. At the opposite extreme, U_i is 0 when species *i* shares exactly the same traits as another species in the pool, in other words is perfectly redundant. U_i scales between 0 and 1 because d_{ij} scales between 0 and 1.

Box 3. Measuring Species Scarcity and Restrictedness

To measure species scarcity within communities we can simply use the inverse of relative abundance with two constraints: the index should range between 0 and 1 to have the same weight as distinctiveness in functional rarity measures (Box 2), and should have a pivotal value of 0.5 for a species with a relative abundance corresponding to $1/N$, N being the number of species in the community. When the relative abundance of species i (Ab_i) is higher than $1/N$ (expectation under the perfect even distribution of abundance among species) the species tend to be dominant while the species tend to be scarcer than expected when $Ab_{i<}$ $1/N$. We can thus express scarcity (Sc) as:

$$Sc_i = exp[-N \times \ln(2) \times Ab_i] \quad \text{(Equation I)}$$

A species with a very low abundance will have a Sc value close to 1 while dominant species (Ab_i close to 1) in species rich communities (N high) will tend to have low values. If $Ab_i = 1/N$ then $Sc_i = 0.5$.

At the regional scale we can measure species restrictedness R using the extent of occurrence or the area of occupancy, the most geographically restricted species have an R value of 1 while widespread species will tend to values close to 0. In this case there is no need to use the pivotal value of $1/N$ because species geographical extents (Ge) are independent. Instead we can use the Ge of the most widespread species to standardize R, which ranges from 0 to 1 [92].

$$R_i = 1 - \frac{Ge_i}{Ge_{max}} \quad \text{(Equation II)}$$

Other rarity indices with multiple cut-off points can also be used [93] to assess species restrictedness, but they are sensitive to species geographic range distributions.

where D_i is the functional distinctiveness of the species and S_i is the species scarcity within a given community. At the regional scale, the FR of species i is expressed as:

$$FR_i = f(U_i, R_i)$$

where U_i is the **functional uniqueness** of species i at the regional scale and R_i is its geographic restrictedness.

The integration of both facets of rarity can be implemented in many ways. The simplest way is to build upon the additive framework that measures the evolutionarily distinct and globally endangered (EDGE) score [63,64]. By analogy, the functional rarity of species i, at a given scale can be estimated as the addition of D_i and S_i at the local scale, or U_i and R_i at the regional scale. This simple integration may be useful in a conservation perspective to provide a comprehensive picture of functional rarity. However, more-complex frameworks can be proposed to combine both facets of rarity to weight them differently or to give a low value if one of the two is low (multiplicative).

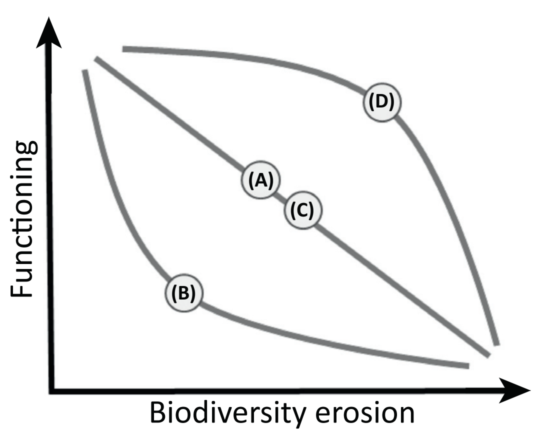
A crucial step is the choice of the traits to be included in the estimation of functional rarity (Box 1). Obviously this depends on the question being investigated. Trait-based theory has identified two types of species traits with respect to their potential functions [44]. 'Effect traits' determine the effect species have on ecosystem functioning, and these are distinguished from 'response traits' which determine the response of species to the environment [44]. This distinction has irrigated many fields of ecology [25] and helps to identify relevant response and effect traits related to the impacts of species on ecosystem functioning, on the one hand, and species persistence and coexistence on the other. From a conservation perspective, it is nevertheless unclear which traits should be accounted for.

Once traits have been chosen for a specific research objective, pairwise species functional distances can be calculated using the Euclidean distance if traits are quantitative (after trait standardization to give the same weight), or using the Gower distance if at least one trait is qualitative or if some values are missing [65]. Many ecological distinctiveness measures have been developed, most of them being designed within a phylogenetic perspective and based on tree branches linking species [66]. By analogy, we propose to measure functional distinctiveness (D_i) and uniqueness (U_i) using a functional space where species are placed according to their traits

(Figure I in Box 1). The main difference between these two measures is that D_i takes into account all species within the community and their abundances, whereas U_i is based on the distance to the functionally nearest species in the regional pool. In other words, distinctiveness assesses whether a species is more or less functionally close to the rest of the community, while uniqueness estimates the extent to which a species has no functional equivalent in the regional pool (Box 2). Box 3 develops how to measure species scarcity and restrictedness.

Functional Rarity and Ecosystem Functioning

Assessing the importance of functional rarity in BEF will require appropriate design to disentangle the effects of species functional distinctiveness and species scarcity. To this end, we propose hypothetical scenarios wherein the influence of biodiversity loss on the shape of BEF relationships (Figure 1) depends on species functional rarity according to the four categories identified at local scale in Figure I. Indeed, if ecosystem functions such as productivity are expected to decrease with biodiversity loss [27], we hypothesize that the shape of this decline will depend on the traits of the first species that is extirpated from the community (Figure 1). When extirpated species support dominant but distinct traits (category B), the functioning will be strongly affected in the first stage of biodiversity decline because irreplaceable traits will be lost. Conversely, this initial impact will be limited when the first extirpated species bear scarce indistinct traits (category D) because the remaining species can perform the same functions. Intermediate relationships are expected when the extirpated species bear either scarce distinct or dominant indistinct traits (categories A and C). The long-term stability of ecosystem functioning [67] should also depend on the traits of species extirpated first, and on the type of traits. The response-effect trait framework has been especially useful for conceptualizing the maintenance (or resilience) of ecosystem functions. When extirpated species support dominant but indistinct (effect) traits (category C), the stability of ecosystem functioning will be strongly affected (loss of functional redundancy). Moreover, distinct (effect) traits (categories A and B) can become the common traits, thus contributing to the long-term assurance of ecosystem functioning [68]. When focusing on the long-term stability, the dynamics of communities is also at play [34], and accounting for response traits is thus of tremendous importance. The loss of species supporting scarce distinct (response) traits (category A) is expected to strongly impact on the long-term stability of ecosystem functioning. To summarize, it is less straightforward to



Trends in Ecology & Evolution

Figure 1. Hypothetical Consequences of Biodiversity Loss on Local Ecosystem Functioning for the Four Scenarios of Functional Rarity (i.e., when species of each group are extirpated first as biodiversity declines). The letters correspond to the categories on the distinctiveness–scarcity biplot at the local scale, as described in Figure I of Box 1.

make qualitative predictions for the stability of ecosystem functioning because response and effect traits are both involved. We encourage ecologists to explore these scenarios theoretically and experimentally. This can come for example from experiments with microorganisms using a dilution protocol where the rare species are lost first [69,70].

Functional Rarity Across the Tree of Life

An evolutionary perspective on functional rarity can shed light on the processes that are at the origin of functional rarity across the tree of life and allow its maintenance. Although no work has been done so far following our suggested framework, there is a long tradition in evolutionary biology to investigate how ecological specializations evolves (e.g., [71,72]). Pioneering work by Futuyma and Moreno [73] has focused on specialization for resource in terms of diet and feeding behavior. However the general hypotheses around a framework to investigate the evolution of functional rarity still need to be developed [74]. Proposing a theoretical evolutionary approach to the integrated view of functional rarity (Figure I) is a long-term perspective. Indeed, both species abundance and trait rarity (functional distinctiveness or uniqueness) are at play. Complex eco-evolutionary models will thus be necessary to answer this question. Examining the phylogenetic signal of trait rarity is a first key step. For instance, the question of whether specialist species or functionally distinct species are also phylogenetically distinct is poorly known (but see [75]). In other words, is there any correlation between functional and

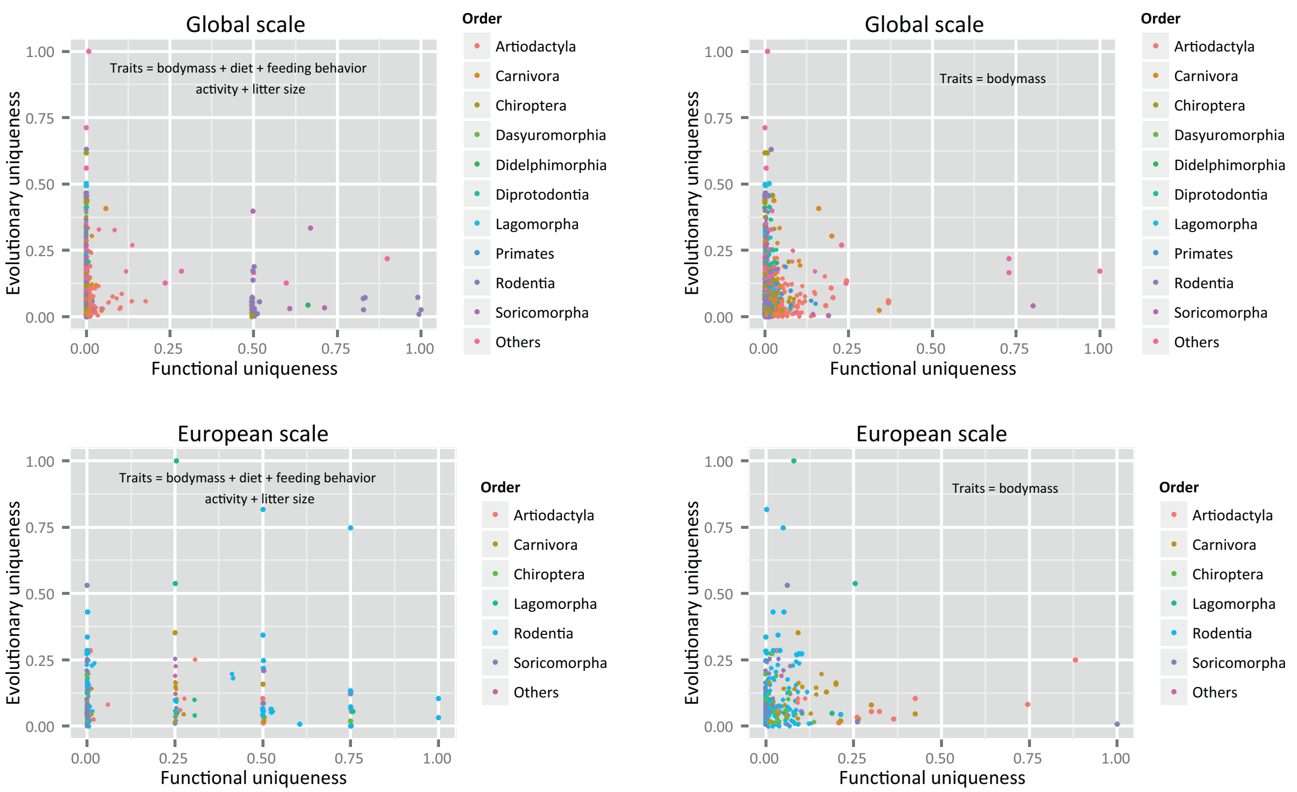


Figure 2. Relationship Between Evolutionary and Functional Uniqueness of Mammals at both Global and European Scales Calculated with Two Different Sets of Traits. All mammals for which both traits and phylogenetic information were available (4616 species) were included. Functional uniqueness was calculated without accounting for abundance. The global mammal functional distance matrices (Gower distance for multiple traits and Euclidean distance for log-transformed body-mass) together with the phylogenetic distances were extracted from [81]. The list of mammal species for Europe was extracted from [82]. Colors represent the 10 and the six most-frequent orders at global and European scales, respectively. The remaining orders (e.g., Monotrema) are grouped into the Others category.

phylogenetic distinctiveness or uniqueness? When examining the global evolutionary and functionally uniqueness of mammals, we did not find species that were both evolutionary and functionally unique (Figure 2). The species pool under study is obviously critical in such relationships, as is the set of traits used to estimate species functional uniqueness (Figure 2, global vs Europe). Interestingly, the shape of the relationship remained stable whether we restricted the analysis to the scale of Europe or to body mass as the sole trait (Figure 2). This can have tremendous consequences for conservation biology [76] in cases where a geographical mismatch between taxonomic, phylogenetic, and functional rarity hotspots is found (see Outstanding Questions). If such pattern is confirmed at the community scale, this will also prevent using phylogenetic distinctiveness as a proxy for functional rarity in BEF research [77], and this will urge functional ecologists to better understand why phylogenetic diversity or dissimilarity matters for ecosystem functioning [78].

Concluding Remarks

Our framework for measuring functional rarity paves the way for an ecology of outliers, which allows a deeper understanding of the role of individuals, genotypes, or species bearing distinct trait values within populations, ecosystems, or biomes. A conservation strategy for ecological outliers can also emerge beyond the identification of areas where functional and evolutionary distinctiveness tend to aggregate [79]. For instance, the effectiveness of protected areas for ecological outliers is still untested, while the conditions (environment, human pressure) under which populations of ecological outliers can persist are unknown. This framework can also contribute to bridging the gap between evolutionary biology and ecology (see Outstanding Questions). A combination of theoretical, observational, and experimental work across the Tree of Life will help to explore this framework and identify the level at which functional rarity should be considered. This work is urgently needed because rare taxa will be the first victims of what is now called the 6th extinction crisis [80].

Acknowledgments

This research is supported by the French Foundation for Research on Biodiversity (FRB; www.fondationbiodiversite.fr) in the context of the CESAB project 'Causes and consequences of functional rarity from local to global scales' (FREE). CV is supported by the European Research Council (ERC) Starting Grant Project 'Ecophysiological and biophysical constraints on domestication in crop plants' (Grant ERC-StG-2014-639706-CONSTRAINTS). WT acknowledges support from the European Research Council (ERC-2011-StG-281422-TEEMBIO).

References

1. Kunin, W. and Gaston, K. (1993) The biology of rarity: patterns, causes, and consequences. *Trends Ecol. Evol.* 8, 298–301
2. Soulé, M. (1986) *Conservation Biology: the Science of Scarcity and Diversity,* Sinauer Associates
3. Gaston, K. (1994) *Rarity,* Chapman & Hall
4. Kunin, W. and Gaston, K. (1997) *The Biology of Rarity: Causes and Consequences of Rare-Common Differences,* Chapman & Hall
5. Soulé, M. (1983) What do we really know about extinction? In *Genetics and Conservation: a Reference for Managing Wild Animal and Plant Populations* (Schonewald-Cox, C. *et al.*, eds), pp. 111–124, Benjamin/Cummings
6. Murray, B. *et al.* (2002) How plant life-history and ecological traits relate to species rarity and commonness at varying spatial scales. *Ecology* 27, 291–310
7. Lavergne, S. *et al.* (2003) Do rock endemic and widespread plant species differ under the leaf-height-seed plant ecology strategy scheme? *Ecol. Lett.* 6, 398–404
8. Gaston, K. and Blackburn, T. (1996) Rarity and body size: generality is important. *Conserv. Biol.* 10, 1295–1298
9. Espeland, E. and Emam, T. (2011) The value of structuring rarity: the seven types and links to reproductive ecology. *Biol. Conserv.* 20, 963–985
10. Jain, M. *et al.* (2014) The importance of rare species: a trait-based assessment of rare species contributions to functional diversity and possible ecosystem function in tall-grass prairies. *Ecol. Evol.* 4, 104–112
11. Walker, B. *et al.* (1999) Plant attribute diversity, resilience and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* 2, 95–113
12. Bracken, M. and Low, N. (2012) Realistic losses of rare species disproportionately impact higher trophic levels. *Ecol. Lett.* 15, 461–467
13. Lyons, K. *et al.* (2005) Rare species and ecosystem functioning. *Conserv. Biol.* 19, 1019–1024
14. Chase, J. (2013) An inordinate foundness of rarity. *PLoS Biol.* 11, e1001573
15. Pendleton, R.M. *et al.* (2004) Loss of rare fish species from tropical floodplain food webs affects community structure and ecosystem multifunctionality in a mesocosm experiment. *PLoS One* 9, e8456
16. Godet, L. *et al.* (2015) Dissociating several forms of commonness in birds sheds new light on biotic homogenization. *Global Ecol. Biogeogr.* 24, 416–426
17. Calba, S. *et al.* (2014) Measuring and explaining large-scale distribution of functional and phylogenetic diversity in birds:

Outstanding Questions

What are the ecological drivers of the maintenance of functional rarity in communities? Elucidating the drivers of functional rarity requires consideration of the effects of both niche-based and neutral community assembly processes [94–97] on both functional distinctiveness and **taxonomic scarcity**. Indeed, niche-based processes affect functional diversity [22,98] – and thus functional distinctiveness – whereas neutral processes influence taxonomic diversity patterns by affecting species demography [99] – and thus relative abundances of species.

Which evolutionary forces generate functional rarity? Future work should not only focus on the relationship between phylogenetic distinctiveness and functional distinctiveness across different clades and regions (Figure 2 for an example), but also investigate the mechanisms that generate such patterns. Focusing on the extremes, it will be fundamental to understand through the lens of evolutionary processes why some old clades could emerge as functionally distinct/unique whereas others do not.

Is there a geographic congruence (or mismatch) of hotspots of taxonomic, functional, and phylogenetic rarity? Mapping functional rarity at a global scale should be a primary objective of functional biogeography [24]. Potential mismatches between the geographic distributions of the different facets of rarity can help to refine priority conservation areas (e.g., [100]).

separating ecological drivers from methodological choices. *Global Ecol. Biogeogr.* 23, 669–678

18. Naeem, S. *et al.* (2012) The functions of biological diversity in an age of extinction. *Science* 336, 1401–1406
19. McGill, B.J. *et al.* (2015) Fifteens forms of biodiversity trend in the Anthropocene. *Trends Ecol. Evol.* 30, 104–113
20. Pereira, H.M. *et al.* (2013) Essential biodiversity variables. *Science* 339, 277–278
21. Rabinowitz, D. (1981) Seven forms of rarity. In *The Biological Aspects of Rare Plant Conservation* (Synge, H., ed.), pp. 205–217, Wiley
22. McGill, B.J. *et al.* (2006) Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* 21, 178–185
23. Shipley, B. (2010) *From Plant Traits to Vegetation Structure. Chance and Selection in the Assembly of Ecological Communities,* Cambridge University Press
24. Violle, C. *et al.* (2014) The emergence and promise of functional biogeography. *Proc. Natl Acad. Sci. U.S.A.* 111, 13690–13696
25. Laughlin, D.C. (2014) Applying trait-based models to achieve functional targets for theory-driven ecological restoration. *Ecol. Lett.* 17, 771–784
26. Cadotte, M.W. *et al.* (2015) Predicting communities from functional traits. *Trends Ecol. Evol.* 30, 500–511
27. Hooper, D.U. *et al.* (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.* 75, 3–35
28. Diaz, S. *et al.* (2007) Functional diversity – at the crossroads between ecosystem functioning and environmental filters. In *Terrestrial Ecosystems in a Changing World* (Canadell, J. *et al.*, eds), pp. 81–91, Springer-Verlag
29. Cadotte, M.W. *et al.* (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. *J. Appl. Ecol.* 48, 1079–1087
30. Power, M.E. *et al.* (1996) Challenges in the quest for keystones. *BioScience* 46, 609–620
31. Isbell, F. *et al.* (2015) The biodiversity-dependent ecosystem service debt. *Ecol. Lett.* 18, 119–134
32. Levine, J. and HilleRisLambers, J. (2009) The importance of niches for the maintenance of species diversity. *Nature* 461, 254–257
33. Roughgarden, J. (1972) Evolution of niche width. *Am. Nat.* 106, 683–718
34. Loreau, M. *et al.* (2003) Biodiversity as spatial insurance in heterogeneous landscapes. *Proc. Natl Acad. Sci. U.S.A.* 100, 12765–12770
35. Low-Décarie, E. *et al.* (2015) Community rescue in experimental metacommunities. *Proc. Natl Acad. Sci. U.S.A.* 112, 14307–14312
36. Solan, M. *et al.* (2004) Extinction and ecosystem function in the marine benthos. *Science* 306, 1177–1180
37. Grime, J.P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* 86, 902–910
38. Ricciardi, A. and Ramussen, J.B. (1999) Extinction rates of North American freshwater fauna. *Conserv. Biol.* 13, 1220–1222
39. Myers, R.A. and Worm, B. (2003) Rapid worldwide depletion of predatory fish communities. *Nature* 423, 280–283
40. Mouillot, D. *et al.* (2013) Rare species support vulnerable functions in high-diversity ecosystems. *PLoS Biol.* 11, e1001569
41. Harnik, P.G. *et al.* (2002) Long-term differences in extinction risk among the seven forms of rarity. *Proc. R. Soc. B* 279, 4969–4976
42. Westoby, M. *et al.* (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annu. Rev. Ecol. Evol. Syst.* 33, 125–159
43. Lavorel, S. *et al.* (2013) A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. *J. Veg. Sci.* 24, 942–948
44. 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
45. Violle, C. *et al.* (2007) Let the concept of trait be functional! *Oikos* 116, 882–892
46. Violle, C. and Jiang, L. (2009) Towards a trait-based quantification of species niche. *J. Plant Ecol.* 2, 87–93
47. Gravel, D. *et al.* (2016) The meaning of functional trait composition of food webs for ecosystem functioning. *Phil. Tran. R. Soc. B.* 371, 20150268
48. Umana, M.N. *et al.* (2015) Commonness, rarity, and intraspecific variation in traits and performance in tropical tree seedlings. *Ecol. Lett.* 8, 1329–1337
49. Leitão, R.P. *et al.* (2016) Rare species contribute disproportionately to the functional structure of species assemblages. *Proc. R. Soc. London Ser. B.* 283, 20160084
50. Thompson, K. *et al.* (2010) Little evidence for limiting similarity in a long-term study of a roadside plant community. *J. Ecol.* 98, 480–487
51. Albert, C. *et al.* (2012) On the importance of intraspecific variability for the quantification of functional diversity. *Oikos* 121, 116–126
52. Jung, V. *et al.* (2010) Intraspecific variability and trait-based community assembly. *J. Ecol.* 98, 1134–1140
53. Zuppinger-Dingley, D. *et al.* (2014) Selection for niche differentiation in plant communities increases biodiversity effects. *Nature* 515, 108–111
54. Siefert, A. *et al.* (2015) A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecol. Lett.* 18, 1406–1419
55. Fontana, S. *et al.* (2015) Individual-level trait diversity concepts and indices to comprehensively describe community change in multidimensional trait space. *Funct. Ecol.* 30, 808–818
56. Violle, C. *et al.* (2012) The return of the variance: intraspecific variability in community ecology. *Trends Ecol. Evol.* 27, 244–252
57. Mason, N.W.H. *et al.* (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* 111, 112–118
58. De Bello, F. *et al.* (2013) Which trait dissimilarity for functional diversity: trait means or trait overlap? *J. Veg. Sci.* 24, 807–819
59. Pavoine, S. *et al.* (2009) On the challenge of treating various types of variables: application for improving the measurement of functional diversity. *Oikos* 118, 391–402
60. Chao, A. *et al.* (2010) Phylogenetic diversity measures based on Hill numbers. *Phil. Trans. Roy. Soc. B.* 365, 3599–3609
61. Mouchet, M. *et al.* (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Funct. Ecol.* 24, 867–876
62. Cadotte, M.W. *et al.* (2013) The ecology of differences: integrating evolutionary and functional distances. *Ecol. Lett.* 16, 1234–1244
63. Cadotte, M. and Davies, T. (2010) Rarest of the rare: advances in combining evolutionary distinctiveness and scarcity to inform conservation at biogeographical scales. *Divers. Distrib.* 16, 376–385
64. Isaac, N.J.B. *et al.* (2007) Mammals on the EDGE: conservation priorities based on threat and phylogeny. *PLoS One* 2, e296
65. Legendre, P. and Legendre, L. (1998) *Numerical Ecology,* Elsevier
66. Redding, D.W. *et al.* (2014) Measuring evolutionary isolation for conservation. *PLoS One* 9, e113490
67. Yachi, S. and Loreau, M. (1999) Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc. Natl Acad. Sci. U.S.A.* 96, 1463–1468
68. Mariotte, P. *et al.* (2013) Subordinate plant species enhance community resistance against drought in semi-natural grasslands. *J. Ecol.* 101, 763–773
69. Peter, H. *et al.* (2011) Function-specific response to depletion of microbial diversity. *ISME J.* 5, 351–361
70. Bouvier, T. *et al.* (2012) Contrasted effect of temporal and spatial insurance in marine bacterioplankton communities. *PLoS One* 7, e37620

71. Bonetti, M.F. and Wiens, J.J. (2014) Evolution of climatic niche specialization: a phylogenetic analysis in amphibians. *Proc. R. Soc. B-Biol. Sci.* 281, 20133229
72. Cornwell, W.K. *et al.* (2014) Functional distinctiveness of major plant lineages. *Funct. Ecol.* 102, 345–356
73. Futuyma, D.J. and Moreno, G. (1988) The evolution of ecological specialization. *Annu. Rev. Ecol. Evol. Syst.* 19, 207–233
74. Fernandez, M.H. and Vrba, E.S. (2005) Macroevolutionary processes and biomic specialization: testing the resource-use hypothesis. *Evol. Ecol.* 19, 199–219
75. Thuiller, W. *et al.* (2015) Conserving the functional and phylogenetic trees of life of European tetrapods. *Phil. Tran. R. Soc. B.* 20140005
76. Winter, M. *et al.* (2013) Phylogenetic diversity and nature conservation: where are we? *Trends Ecol. Evol.* 28, 199–204
77. Srivastava, D. *et al.* (2012) Phylogenetic diversity and the functioning of ecosystems. *Ecol. Lett.* 15, 637–648
78. Cadotte, M.W. (2013) Experimental evidence that evolutionarily diverse assemblages result in higher productivity. *Proc. Natl Acad. Sci. U.S.A.* 110, 8996–9000
79. Jetz, W. *et al.* (2014) Distribution and conservation of global evolutionary distinctness in birds. *Curr. Biol.* 2014, 919–930
80. Ceballos, G. *et al.* (2015) Accelerated modern human-induced species losses: entering the sixth mass extinction. *Science Adv.* 1, 1–5
81. Mazel, F. *et al.* (2014) Multifaceted diversity–area relationships reveal global hotspots of mammalian species, trait and lineage diversity. *Global Ecol. Biogeogr.* 23, 836–847
82. Zupan, L. *et al.* (2014) Spatial mismatch of phylogenetic diversity across three vertebrate groups and protected areas in Europe. *Divers. Distrib.* 20, 674–685
83. Kattge, J. *et al.* (2011) TRY: a global database of plant traits. *Global Change Biol.* 17, 2905–2935
84. Dell, A.I. *et al.* (2013) Trait database for size and temperature dependence of species ineractions. *Ecology* 94, 1205–1206
85. Wilman, H. *et al.* (2014) EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. *Ecology* 95, 2027–2027
86. Homburg, K. *et al.* (2014) Carabids.org – a dynamic online database of ground beetle species traits (Coleoptera, Carabidae). *Insect Conserv. Divers.* 7, 195–205
87. Sandel, B. *et al.* (2015) Estimating the missing species bias in plant trait measurements. *J. Veg. Sci.* 26, 828–838
88. Violle, C. *et al.* (2015) Trait databases: misuses and precautions. *J. Veg. Sci.* 26, 826–827
89. Violle, C. *et al.* (2015) Vegetation ecology meets ecosystem science: permanent grasslands as a functional biogeography case study. *Sci. Tot. Env.* 534, 43–51
90. Buisson, L. *et al.* (2013) Toward a loss of functional diversity in stream fish assemblages under climate change. *Global Change Biol.* 19, 387–400
91. Webb, C.O. *et al.* (2002) Phylogenies and community ecology. *Annu. Rev. Ecol. Evol. Syst.* 33, 475–505
92. Dapporto, L. and Dennis, R.L.H. (2008) Species' richness, rarity and endemicity of Italian offshore islands: complementary signals from island-focused and species-focused analyses. *J. Biogeogr.* 35, 664–674
93. Leroy, B. *et al.* (2012) Improving occurrence based rarity metrics in conservation studies by including multiple rarity cut-off points. *Insect Conserv. Divers.* 5, 159–168
94. Adler, P. *et al.* (2007) A niche for neutrality. *Ecol. Lett.* 10, 95–104
95. Vergnon, R. *et al.* (2009) Niches versus neutrality: uncovering the drivers of diversity in a species-rich community. *Ecol. Lett.* 12, 1079–1090
96. Holt, R.D. (2006) Emergent neutrality. *Trends Ecol. Evol.* 21, 531–533
97. Gravel, D. *et al.* (2006) Reconciling niche and neutrality: the continuum hypothesis. *Ecol. Lett.* 9, 399–409
98. Enquist, B.J. *et al.* (2015) Scaling from traits to ecosystems: developing a general trait driver theory via integrating trait-based and metabolic scaling theories. *Adv. Ecol. Res.* 52
99. Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography,* Princeton University Press
100. Devictor, V. *et al.* (2010) Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. *Ecol. Lett.* 13, 1030–1340