

## REVIEW

## Defining and measuring ecological specialization

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## Summary

1. Ecological specialization is one of the main concepts in ecology and conservation. However, this concept has become highly context-dependent and is now obscured by the great variability of existing definitions and methods used to characterize ecological specialization.

2. In this study, we clarify this concept by reviewing the strengths and limitations of different approaches commonly used to define and measure ecological specialization. We first show that ecological specialization can either be considered as reflecting species' requirements or species' impacts. We then explain how specialization depends on species-specific characteristics and on local and contingent environmental constraints. We further show why and how ecological specialization should be scaled across spatial and temporal scales, and from individuals to communities.

3. We then illustrate how this review can be used as a practical toolbox to classify widely used metrics of ecological specialization in applied ecology, depending on the question being addressed, the method used, and the data available.

4. *Synthesis and applications.* Clarifying ecological specialization is useful to make explicit connections between several fields of ecology using the niche concept. Defining this concept and its practical metrics is also a crucial step to better formulate predictions of scientific interest in ecology and conservation. Finally, understanding the different facets of ecological specialization should facilitate to investigate the causes and consequences of biotic homogenization and to derive relevant indicators of biodiversity responses to land-use changes.

**Key-words:** biotic homogenization, ecological niche, Elton, Grinnell, Hutchinson, indicator, niche breadth, niche metrics, specialist-generalist, species distribution models

## Introduction

Specialist species are increasingly shown to be declining and experiencing higher extinction risk relative to generalist species (Clavel, Julliard & Devictor, in press). Specialists are often even considered to be the 'great losers' of past and current global changes (McKinney 1997; Devictor *et al.* 2008; Colles, Liow & Prinzing 2009), and trends in the abundance of these species are used as indicators of unsustainable development at national and international scales (Gregory *et al.* 2005).

Meanwhile, an increasing number of specialization indices have been proposed in the literature. For instance, specialization is inferred indirectly from species distributions and envi-

ronmental data (Calenge & Basille 2008), or from direct measures of species performances in multiple environments (Kassen 2002). Alternatively, highly detailed measures of dietary specialization have indicated that not only species, but also individuals within a species, are more or less specialized (Bolnick *et al.* 2003). The quantification of ecological specialization is also highly dependent on the data used, the organism studied, and the ecological mechanism of interest (e.g. behaviour specialization vs. specialization for habitat). Consequently, each publication studying ecological specialization has virtually redefined the concept (Ferry-Graham, Bolnick & Wainwright 2002).

The term 'specialization' is also now used inconsistently throughout the ecological literature for different biological levels (individual, species, population or community) and measured at very different spatial scales. Although flexibility in

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the definition of ecological specialization can be facilitative, it could also cause confusion that should be clarified for applied purposes.

Concepts of specialist vs. generalist species have a long history in theoretical and applied ecology. In the pioneering theoretical literature, ecological specialization was most often synonymous with a limited niche breadth, resulting from evolutionary trade-offs between the ability of species to exploit a range of resources and their capacity to use each one (the 'jack-of-all-trades is master of none' hypothesis; MacArthur 1972). Specialization has also been outlined previously as a key concept to predict the adaptive response of populations in heterogeneous and/or fluctuating environments (Levins 1968).

Subsequently, the concept of ecological specialization received several clarifications. In particular, in their seminal review of ecological specialization, Futuyma & Moreno (1988) emphasized the need to clarify specialization from the classical distinction between the fundamental niche of a species and its realized niche (Hutchinson 1957). Pulliam (2000) further stressed the need to account for dispersal processes when inferring niche characteristics from species distribution: species might be found in unsuitable habitats because of source-sink dynamics or be absent from suitable habitats because of dispersal limitation (Thomson *et al.* 1996).

Although these clarifications have increased our understanding of the concept of specialization, a classification of the numerous existing definitions and metrics of ecological specialization is missing. In this study, we first highlight the most commonly used definitions of ecological specialization. We then identify why and how specialization should be quantified across various spatial and temporal scales, and from individuals to communities. We further propose a flexible toolbox for measuring ecological specialization depending on the data available and the questions addressed. Based on this review, we illustrate how using different facets of ecological specialization can motivate timely research directions in several fields of ecology.

## Finding common ground in widely used definitions of ecological specialization

### GRINNELLIAN VS. ELTONIAN SPECIALIZATION

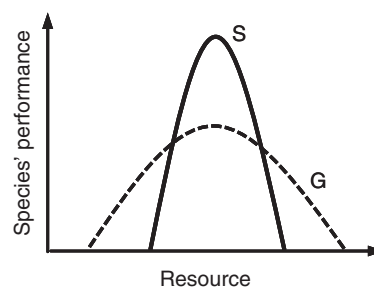
Ecological specialization is often defined as the restricted ecological niche breadth (or width) of a given species (Futuyma & Moreno 1988). As such, clarifications of the niche concept have repeatedly emphasized the need to discern *Grinnellian* from *Eltonian* dimensions of the niche (Chase & Leibold 2003; Guisan & Thuiller 2005; Soberón 2007). The Grinnellian niche describes *the response of species to a given set of variables*, here considered as resources (Grinnell 1917), while the Eltonian niche (sometimes called functional or trophic-niche) focuses on *the impact of species in the environment* rather than on its response to particular resources (Elton 1927).

Grinnellian niche can be further extended to Hutchinson's (1957) concept of the ecological niche (which has been the most influential concept) where all biotic and abiotic resources are

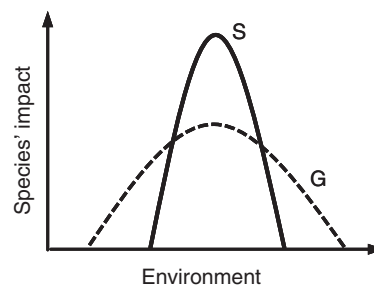
considered. In this case, the niche is generally defined as a hyper-volume in the multidimensional space of ecological variables, within which a species can maintain a viable population (Hutchinson 1957). Similarly, the Eltonian-niche concept can be extended in an  $n$ -dimensional functional space, measured as the species position along axes embodying functional attributes, rather than resource variables (Rosenfeld 2002; Mouillot, Mason & Wilson 2007). This functional conception of the ecological niche has recently received new theoretical and methodological attention following the growing interest for functional traits in community and applied ecology (McGill *et al.* 2006; Ackerly & Cornwell 2007).

Based on this first distinction between the two classes of ecological niche, the *Grinnellian specialization* of a species should represent the variance in species' performance across a range of environmental conditions, broadly defined by one or several biotic (and/or abiotic) resources (Fig. 1a). Note that, in practice, Grinnellian specialization can be defined as the breadth of species requirement using the term 'resource' in its largest sense. For instance, habitat-specialization can be a proxy for Grinnellian specialization if habitat is not only the physical place where the species is found but encompasses conditions that influence species' performance in various ways (e.g. species might need specific habitat for reproduction, predator refuges or specific food requirements). More generally,

(a) Grinnellian specialization



(b) Eltonian specialization



**Fig. 1.** Definition of Grinnellian vs. Eltonian specialization. (a) The Grinnellian specialization of a given species can be described by its variance in performance across a given range of resources. For a given mean performance, the dashed line describes the performance of a generalist species (generalist, G) and the solid line of a more specialist species (specialist, S). (b) Eltonian specialization is defined as the variance in the species' impact (instead of performance) on the environment. For a given mean impact, the species' impact can be distributed through a large part of the environment (G) or be more restricted (S).

Grinnellian specialization reflects the range of each biotic and abiotic factor determining the distribution and abundance of a single species and is most often measured using species' requirements for non-interactive variables (Soberón 2007).

In the Eltonian concept of niche, each species has a particular role in an ecosystem. For instance, according to Elton, there are detritivorous, dispersal or pollination niches (Elton 1927). Therefore, this functional niche refers to a species position in ecological networks, and is often used in functional ecology and ecosystem ecology. This definition is also closely related to the concept of 'guild' or 'functional groups' which aggregates species according to their trophic relationships with the biotic environment (e.g. scavengers, grazers and seed eaters). Therefore, the *Eltonian specialization* refers to the functional position of species in its environment and is measured as the species breadth of functional roles (that we consider a synonym of impact) instead of resource used (Fig. 1b). Elton historically assimilated the niche of a species to its 'place in the biotic environment, its relations to food and enemies' so that the functional role of the focal species most usually refers to its impacts on other species (e.g. pollination, predation and herbivory). However, abiotic changes generated by the focal species can also be considered (e.g. oxygen generation, carbon dioxide acquisition and mineralization) as they indirectly impact on other species in the ecosystem.

Discerning Grinnellian from Eltonian specialization in applied ecology is thus essentially a practical way to emphasize the difference between the breadth of species' requirements (what the species *needs*) and the breadth of species' effects on the environment (what the species *does*). This basic distinction does not *a priori* depend on a particular scale or the data used and should be relevant to any species. This traditional classification is far from being complete or flawless (see Discussion and implications). However, the distinction between Eltonian and Grinnellian specialization sets a meaningful heuristic basis which includes most specialization definitions used with empirical data in applied ecology.

#### FUNDAMENTAL VS. REALIZED SPECIALIZATION

Beyond the distinction between Grinnellian vs. Eltonian-niche, the concept of specialization can be further clarified using the classical distinction between the fundamental and realized niche (Hutchinson 1957). Indeed, both Grinnellian and Eltonian specialization can be usefully considered as an intrinsic species attribute (fundamental), or alternatively, as a contingent property dependent on abiotic and biotic environments (realized). If no distinction is made between realized and fundamental specialization, then disentangling specialization resulting from local adaptation, as opposed to apparent specialization resulting from competitive exclusion and/or source-sink dynamics becomes more difficult.

In practice, the two dimensions (Grinnellian vs. Eltonian and realized vs. fundamental) must be seen as the extremes of a continuum. Each dimension emphasizes a particular aspect of the ecological niche which often corresponds to different objectives and involves different methods.

## Ecological specialization across spatial, temporal and ecological scales

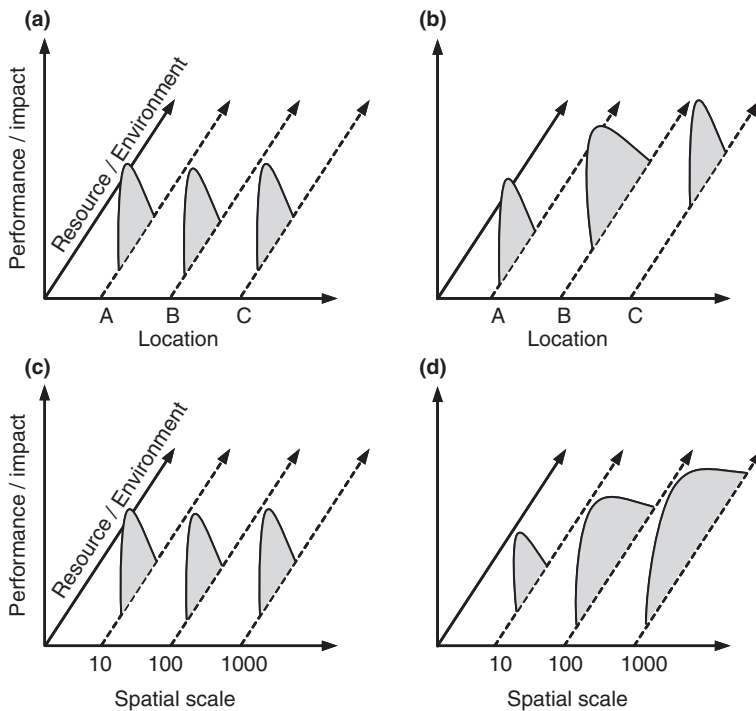
### SPATIAL AND TEMPORAL DEPENDENCE OF ECOLOGICAL SPECIALIZATION

Regardless of its particular definition, the great flexibility of the specialization concept has also led to definitions and measurements of specialization at various spatial and temporal scales. The ecological specialization is indeed always implicitly conditioned to a set of resources (or type of impact) considered, and to the spatial and temporal scale at which it is evaluated. Similarly, the realized specialization of a given species measured at a given point in time may only reflect a subsample of what conditions the species can experience during a longer time-period (or a subsample of their functional role). Surprisingly, although this problem of scaling is recurrent and inherent to most ecological patterns and process, ecological specialization is generally treated and quantified as insensitive to differences in temporal and spatial scales.

In fact, whether the realized Grinnellian or Eltonian specialization is found to be constant across locations for a given species mostly depends on four mechanisms which may or may not promote the shift in niche breadth: (i) the spatial and temporal fluctuation of environmental conditions and species interactions; (ii) local genetic adaptations; (iii) phenotypic plasticity of individuals; or (iv) the sampling design itself if different environmental conditions are sampled across the locations considered. Specialization may therefore be found to be constant across locations if similar environmental conditions are sampled and if individuals have not experienced different local adaptations (Fig. 2a). Alternatively, the realized specialization may vary across locations if different environmental conditions are sampled in the field and/or if individuals have experienced different local adaptations across these locations (Fig. 2b).

Similarly, a particular species which appears locally specialized for any ecological factor can be found to be equally specialized at larger spatial scales (Fig. 2c). For instance, Krasnov *et al.* (2008) found a scale-invariant pattern in the relationships between local and global host specificity (a measure of niche breadth for parasites). Alternatively, a scale-dependence of ecological specialization is often induced by a sampling effect: increasing the scale of observation increases the number of resources present and used (as well as the breadth of possible functional roles) so that niche breadth can show a monotonic positive relationship with the scale of observation (Fig. 2d).

The spatial and/or temporal scaling of ecological specialization not only raises methodological issues (e.g. when seeking for unbiased measures of specialization) but also important ecological processes involved in species' response to global changes. Indeed, Levins (1968) has previously shown that the fate of individuals of more or less specialized species is highly dependent on whether temporal and/or spatial environmental fluctuations are occurring at high frequency (fine-grained) and at low frequency (coarse-grained). This difference in the timing of environmental fluctuations (or in the spacing between environmental conditions) should influence both Grinnellian and



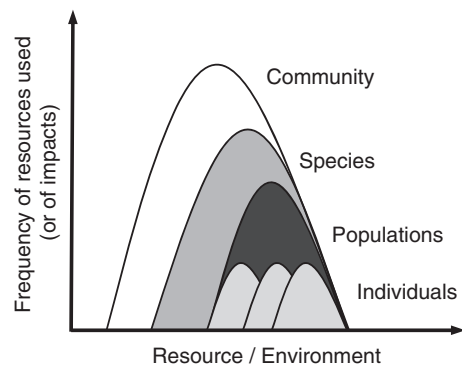
**Fig. 2.** Spatial dependence of specialization. (a) Specialization is often considered as an invariant species-property that is consistent across locations. (b) Alternatively, species may have different levels of specialization in varying locations. This spatial dependence of niche breadth can be induced by true shift in specialization across locations, or by variable resource availability. A spatial dependence can also be observed when the scale at which specialization is measured increases (c, d).

Eltonian specialization. If environmental conditions experienced by individuals are relatively constant during their lifetime (coarse-grain fluctuations), local adaptations will favour individuals with higher level of Grinnellian specialization (Levins 1968). Similarly, the effects of coarse vs. fine-grained environmental variation can influence different functional traits and the realized Eltonian specialization of individuals (e.g. variation in water regime on plants; Engelmann & Schlichting 2005).

#### FROM INDIVIDUAL TO COMMUNITY SPECIALIZATION

The concept of specialization was historically developed as a species attribute (but see Roughgarden 1972), however, it can be extended to any ecological level (individual, population, species and community) for applied or management issues (Fig. 3). Indeed, some species that are considered as ecological generalists are often heterogeneous collections of specialized individuals (Bolnick *et al.* 2003). This within-species variation of ecological specialization can have important conservation implications. For instance, increasing the proportion of a particular resource for a species of conservation interest would only benefit individuals which are specialized to this particular resource.

At the community level, specialization can be estimated as the mean specialization of species present in that community and may be used to derive indicators of conservation interest. For example, the Community Specialization Index reflects the relative abundance of more or less specialized species in a given community (Devictor *et al.* 2008). This indicator has been shown to be powerful and robust in reflecting community response to spatial and temporal disturbance (Devictor & Robert 2009). Similarly, specialization can be defined for any



**Fig. 3.** Ecological specialization from individuals to communities. Both Grinnellian and Eltonian specialization can be usefully defined at any ecological level. A specialized community is composed of a range of more or less specialized species, which are themselves composed of more or less specialized populations, which are finally composed of a range of individuals with differing degrees of specializations.

aggregated ecological level such as species interaction networks (Blüthgen *et al.* 2008), food webs and ecosystems (Dunne, Williams & Martinez 2002).

#### SCALING-UP ECOLOGICAL SPECIALIZATION

Obviously, there is no single appropriate spatial, temporal or ecological scale to measure ecological specialization. Instead, the relevance of any scale will depend on the objective. However, describing the spatial and/or temporal scale-dependence of specialization as well as its variations between ecological levels (from individuals to community) can be very useful. In this respect, Pickett & Bazzaz (1978) suggested that, by analogy

with the classical partitioning of regional diversity, ecological niche can be partitioned into local scale (at which interactions among species occur,  $\alpha$ -niche) and regional scale (measured across multiple sites,  $\beta$ -niche) components. Hughes (2000) have also proposed that specialization measured at any scale can be partitioned into local ( $\alpha_s$ ) and regional ( $\gamma_s$ ) components. The local and regional specialization can be further related to each other by the between-scale specialization ( $\beta_s = \gamma_s/\alpha_s$ ). Then, this partitioning can be used to distinguish between species which are generalists at any spatial scale from those that are generalists locally but that appear to be specialists at larger scales (e.g. if these species use many resources within habitats, but have a low turnover of resources use among habitats) (Hughes 2000).

Interestingly, a similar approach can also be used to scale ecological specialization across ecological levels. Indeed, the total niche breadth measured at any ecological level can be subdivided into a within-level component and a between-level component. In this respect, Roughgarden (1972) proposed to define the total niche width of a population ( $TNW$ ) as the sum of, respectively, a within and a between individual component (traditionally called  $WIC$  and  $BIC$ ). This approach was successfully used to assess how much variation in a total apparent specialization ( $TNW$ ) can be explained by variation within or between individuals (i.e. by calculating  $WIC/TNW$ ) (Sargeant 2007).

We suggest that this scaling-up of ecological specialization could be extended to any type of specialization (Eltonian and Grinnellian) and for any ecological level. For instance, for Eltonian specialization an explicit partitioning of species traits into alpha and beta components can be used (Ackerly & Cornwell 2007). This second type of scaling (i.e. across ecological levels) should also be facilitative to investigate the drivers of variation of ecological specialization across space and time.

## A toolbox for measuring ecological specialization

### GENERAL PRINCIPLE AND WIDELY USED APPROACHES

According to the general definitions of ecological specialization (Fig. 1), measuring niche breadth requires an understanding of (i) what environmental conditions individuals can experience (or what is the extent of their impact for Eltonian specialization) and (ii) how the performance of individuals (i.e. growth, survival and reproduction) is affected by those environmental conditions (or what are the strengths of their impacts). Generally, the practical ways of measuring specialization do not match these theoretical definitions. For example, in the Eltonian view of the niche, each species has a special role. However, this definition neither provide a clear formal quantification of what should be taken as the actual species' 'role' nor of its specificity. Therefore, when functional groups are delineated using this view, or when a species is considered to be specialized in terms of its functional traits relative to other species, Eltonian niche simply describes the degree of

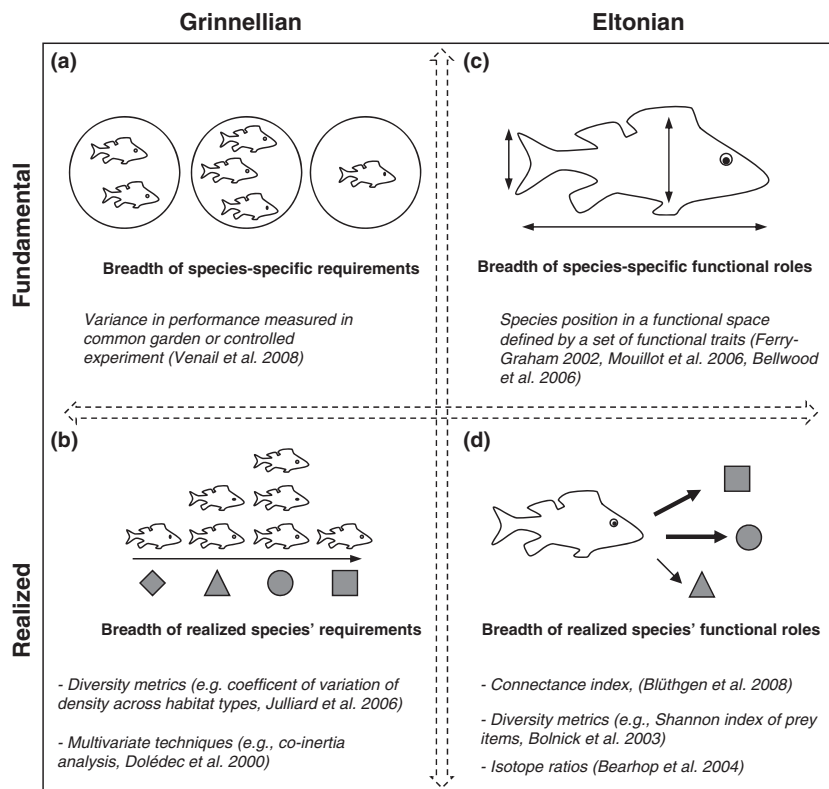
'being special'. The breadth of impact is then inferred from its 'functional distance' to other species, or from the species position in an interacting network, but is hardly quantified directly.

In practice, measuring what environmental conditions individuals are experiencing (or impacting) faces two additional challenges. First, one needs to select a number of meaningful variables most likely to influence species' performances (or to represent species' impacts). Secondly, the measurement of those variables, along with the quantification of variations in species' performances (or impact), must be unbiased. To overcome these technical constraints, many studies classify species as specialist or not according to arbitrary criteria. When continuous metrics are proposed, they are more or less related to simple approaches reflecting species' needs or species' roles (see Fig. S1, Supporting information). However, in the growing literature of applied and conservation ecology, depending on the question being addressed and on the data available, many other measures of ecological specialization have been proposed at various ecological and spatial scales (see below). We suggest that our review can be turned into a practical and flexible toolbox which encompasses most of the widely used metrics of ecological specialization.

### FUNDAMENTAL GRINNELLIAN SPECIALIZATION

To measure fundamental Grinnellian specialization (Fig. 4a), any measure of niche breadth can be used as soon as the species' performances are reflecting robust species-specific characteristics rather than particular species' requirements contingent to local and temporal situations. Ideally, Fundamental Grinnellian specialization should therefore be derived from controlled experiment in which species' performances are measured separately across several resources (e.g. common garden experiment; Venail *et al.* 2008) or along a controlled resource gradient (Wright *et al.* 2006). Instead, *a priori* knowledge of species-specific requirements is often used to produce *ad hoc* classification of ecological specialization level (e.g. by attributing an increasing score of specialization from the less to the most specialized species) and considering this specific attribute as a fixed species' characteristic.

Whether or not species distribution models can be used to approximate the fundamental Grinnellian niche at large scales is frequently debated (Guisan & Thuiller 2005; Kearney 2006; Soberón 2007). On the one hand, the species' fundamental Grinnellian niche could be considered to be more influenced by large-scale bioclimatic variables than between-species interactions (Soberón 2007). Hence, to some extent, species distribution models could be used to approximate the fundamental Grinnellian specialization. On the other hand, large-scale empirical data used in any species distribution model are themselves implicitly shaped by biotic interactions, dispersal limitation and limiting resources (Guisan & Thuiller 2005). As such, they cannot be used to represent the fundamental niche (Kearney 2006). An alternative and emerging research direction for the approximation and the mapping of the fundamental niche is to integrate mechanistic trait-based approaches to



**Fig. 4.** A toolbox for widely used metrics of ecological specialization. Most commonly used metrics of specialization can be positioned in this box according to the type of niche considered (Grinnellian vs. Eltonian) and whether the fundamental or the realized specialization is measured. Note that this typology is flexible (i.e. the dashed arrows underline that specialization metrics are often not belonging to a unique class but rather delineate a continuum). The figure represents a fish for which specialization is measured using different metrics: (a) the variation in species' performance in a controlled experiment (three different conditions are represented by three circles) will reflect its fundamental Grinnellian specialization; (b) the variation in performance along different resource categories (symbolized by geometrical items) using field data will reflect the realized Grinnellian specialization; (c) the fundamental Eltonian specialization would be derived from metrics based on the species-specific functional traits. (d) Finally, the realized Eltonian specialization will be quantified using the diversity and strength of impact of the species on others (symbolized by geometrical items).

species distribution models (e.g. accounting for species-specific physiological constraints or other known aspects of the fundamental niche) (Kearney & Porter 2004).

#### REALIZED GRINNELLIAN SPECIALIZATION

The realized Grinnellian specialization (Fig. 4b) is most often quantified using the diversity of resources used by a species in the field. A single resource can be explicitly considered (breadth of light conditions and food-resource) or implicitly encapsulated within discrete categories (e.g. 'habitat' classes). Such measures of specialization implicitly focus on species' requirements, but make no distinction between strong interactions and weak or occasional ones and ignore variation in species' performance. To further account for variation in resource used and/or species' performance, the most widely used metrics of realized Grinnellian specialization have incorporated resource frequency (and/or variation in species' abundances or densities, considered as a proxy for performance) in traditional diversity indices (e.g. Shannon, Simpson indices or coefficient of variation). Using this approach, there are many ways to measure specialization, but all are related to the simplest

estimation provided by Levin's niche breadth (Fig. S1a, Supporting information).

These simple metrics have become very popular measures of ecological specialization because they are easy to explain and calculate. However, they are prone to sampling biases and pitfalls, long known to obscure estimates of diversity. One of the well-known (although often ignored) problems of measuring specialization using this approach is the integration of resource availability. As previously noted by Colwell & Futuyma (1971), this problem simply results from the fact that 'the koala is really a generalist on Eucalyptus leaves, while the Virginia opossum is specialized for eating garbage'. With most diversity metrics, the use of rare resources is given the same weight as the use of common ones. Therefore, these indices cannot discriminate species with strong shifts in resource preferences from those using resources simply in proportion to their occurrence in the environment (Feinsinger, Spears & Poole 1981). In this case, specialization metrics cannot be considered as reflecting species' requirements but are a complex and obscure mixture between true specialization and resource distribution.

In fact, most simple specialization metrics can be severely biased by the way resources are classified or weighed, and/or if

the range, nonlinearity and spacing of the resource are not appropriately sampled (Colwell & Futuyma 1971). If these problems are not corrected, specialization of species occurring in few samples can be biased (the most classic artefact is that rare species systematically tend to be specialized).

Different approaches have been suggested to deal with these problems which all have their costs, biases and strengths. First, diversity indices (e.g. Simpson or Shannon indices) can be adapted to account for resource availability (Feinsinger *et al.* 1981; Smith 1982). Secondly, resource utilization can be defined based on an explicit distinction between the raw proportion of a given resource and the proportion of the same resource standardized by its relative availability (so-called 'electivity') (Winemiller & Pianka 1990).

The realized Grinnellian specialization metrics could also be derived from species distribution models (reviewed in Guisan & Thuiller 2005) or multivariate analyses (ter Braak 1986; Dolédec, Chessel & Gimaret-Carpentier 2000; Calenge & Basille 2008). Although not being specifically developed to measure specialization, these approaches can make significant contributions to specialization metrics in applied ecology. First, it is relatively simple to extract usual niche characteristics with the use of parametric generalized linear models fitting a unimodal response curve (an optimum and a variance around the optimum, Austin, Nicholls & Margules 1990). Using this approach, measures of niche breadth can be derived from generalized linear models applied to presence-absence or abundance data.

Secondly, most of the multivariate analyses such as canonical correspondence analysis (CCA; ter Braak 1986), redundancy analysis (RDA; ter Braak 1987) or co-inertia analysis (Dolédec *et al.* 2000) can be used to analyse, represent and measure niche characteristics. The two characteristics which are easily extracted from these techniques are niche position that measures marginality in species habitat distribution, and niche breadth, that measures amplitude in species habitat distribution and which can be considered as a measure of Grinnellian realized specialization.

The main advantages of these multivariate approaches from applied perspectives are that they remove collinearity among variables and implicitly search for the most influential combination of variables, and the maximization of species' niche separations. Their drawbacks mostly lie in their underlying hypotheses that are not always met with ecological data. For instance, CCA was originally developed to separate species niches along environmental gradients under the assumption of unimodal response curves. It is therefore particularly adapted to situations in which limiting factors correspond to large gradients. Similarly, RDA has been used for analysing linear relationships between species and gradient, and is therefore more adapted to situations where short portions of the responses can be approximated by straight lines. Unlike the former two methods, co-inertia analysis makes no assumption about the shape of species response curves to the environment and gives equal weight to species-rich and species-poor sites (Dolédec *et al.* 2000), making this technique well suited to measure species' specialization in

many different situations (Thuiller, Lavorel & Araújo 2005; Calenge & Basille 2008).

#### FUNDAMENTAL ELTONIAN SPECIALIZATION

The fundamental Eltonian specialization reflects the intrinsic breadth of species' functional role and is generally measured using its species-specific functional, morphological and/or behavioural traits (Fig. S1b, Supporting information). In this respect, Bellwood *et al.* (2006) proposed measuring the 'morphological specialization' of labrid fishes from a Principal Component Analysis performed on morphological traits involved in trophic interactions (e.g. body mass, mouth gape and mandibulae muscle mass). The specialization of a focal species is then defined as its functional distance (according to its traits) from the centre of gravity of a species pool (Bellwood *et al.* 2006; Mouillot *et al.* 2007).

In these approaches (Fig. 4c), measuring functional traits generally does not tell whether the traits of interest have any relationship to an actual species' performance or what is the real species' impact (Ferry-Graham *et al.* 2002). Alternatively, measuring fundamental Eltonian specialization can explicitly use specific effect traits directly reflecting the ability of the species to perform a particular impact (e.g. specific leaf area and plant height are highly correlated to competitive strength for light). Note that in any case, measuring fundamental Eltonian specialization using averaged species characteristics is generally silent on the realized Eltonian specialization of particular individuals in the field, and is also silent on their actual requirements (Grinnellian specialization).

#### REALIZED ELTONIAN SPECIALIZATION

The realized Eltonian specialization of a given species (Fig. 4d) is most often measured as the number of partners or 'links' between the focal species and others (e.g. number of prey items and number of pollinator species visiting a flowering plant), or in more complex connectance metrics (Blüthgen *et al.* 2008). Interestingly, in case of mutualistic interaction networks (e.g. pollinators and plants), measuring the specialization of each side of the network often reveals asymmetric specialization (Bascompte *et al.* 2003). Accounting for this asymmetry (instead of focusing on the specialization of one side only) can be facilitative to better describe whether and how species are affected by disturbance (Ashworth *et al.* 2004).

When quantifying specialization of interaction networks, the number of interactions between the focal species and others is most often simply counted, ignoring variation in the strength of interactions (Blüthgen *et al.* 2008). Alternatively, as for Grinnellian specialization, diversity metrics (e.g. Simpson or Shannon Diversity Index) can be used to include variations in interaction frequency between a focal species and its interacting partners. These indices can also be adapted to account for the availability of the interacting partners (e.g. the availability of prey for a predator; Sargeant 2007).

As most of measured species' impacts result from 'snapshots' of interactions between species at a point in time, tracking stable isotopes has also become a common alternative to estimate the realized Eltonian specialization, providing for time- and space-integration of the trophic ecology of organisms (Bearhop *et al.* 2004). According to this approach, a more Eltonian generalist species should interact with a larger breadth of species and have more variation in its isotope composition.

Note that although Eltonian niche can ideally be defined as the breadth of impact of a focal species on others (or more generally in the environment), most existing approaches of Eltonian niches cover at most a potential of an impact (fundamental or realized), but rarely the impact itself. While measuring Grinnellian specialization have benefited from many technical and empirical studies, more research is needed to quantify real Eltonian niches.

#### FLEXIBLE AND INTEGRATIVE METRICS

As discussed above, the literature on ecological specialization (applied and theoretical) is structured according to whether specialization is seen as the breadth of species-specific requirements or of species-specific roles. Most widely used metrics of realized specialization directly reflect this distinction. However, we have shown that particular metrics can be used as reflecting either Eltonian or Grinnellian specialization. For instance, diversity metrics (e.g. traditional Shannon index) can be used to quantify the diversity of impacts or of requirements. Similarly, connectance index can be used to quantify the number and complexity of links between species (i.e. specialization is seen as a specific role) rather than species' needs, or, on the contrary, to mirror species' requirements in terms of their interacting partners. Therefore, the difference between Grinnellian and Eltonian specialization is more objective-dependent than conditioned on the use of a particular metric.

Although specialization is inherently dependent on the variables considered (a species can be specialized for a given resource and generalist for others), most studies measure specialization along a unique niche dimension (e.g. specialization along a resource gradient or for habitats). However, one may be interested in integrating the multidimensional nature of the niche. In this case, a principal coordinate analysis (PCoA) can be used. This method allows species to be positioned in a reduced Euclidean space according to a distance matrix describing pairwise distance between species. Interestingly, this distance matrix can be derived from the Gower distance which can be calculated with all types of variables (qualitative, quantitative or a combination of both, also allowing missing data). This method can be used for Eltonian specialization (with variables describing species impacts) or Grinnellian specialization (with variables describing species requirements). The specialization of a focal species can then be defined either as its distance from the centre of the PCoA or by the multidimensional volume filled by its individuals (Carnes & Slade 1982; Mouillot *et al.* 2007). Similarly, the specialization of a community can

be estimated by the multidimensional volume filled by its species.

## Discussion and implications

#### LIMITS IN USING THE TRADITIONAL NICHE CONCEPTS TO MEASURE SPECIALIZATION

Ecological specialization is one of the most versatile concepts in ecology. Given the multidimensional and the multi-scale nature of niches, it can, by definition, never be fully quantified (Colwell & Futuyma 1971). Moreover, there are several limits in using the concept of ecological niche in applied ecology. Ecological niche has evolved semantically following the maturation of ecological concepts and paradigms as well as following the increase in statistical tools to measure niche dimensions. Given this complex historical development and its multiple (often conflicting) interpretations, new *ad hoc* definitions of ecological niche are frequently proposed in applied ecology, with no strong connection with ecological theory (Milesi & López de Casenave 2005).

In reviewing how ecological specialization is generally defined and measured, we have highlighted the limits and values of various definitions and metrics of specialization, rather than proposing a unique definition. We have also shown that the need for explicit distinctions between Eltonian and Grinnellian specializations is context-dependent. Indeed, whether interaction between a given species and particular resources is considered as a species' requirement or as a species' impact is more a point of view than a clear and objective distinction. Moreover, measuring functional traits can both reflect potential species requirement (i.e. a response trait) and potential species impact (i.e. an effect trait; Lavorel & Garnier 2002).

In this context, Chase & Leibold (2003) proposed that ecological niche could alternatively be viewed as an irreducible product of the species–environment interaction resulting from both species' impacts and requirements. This is particularly relevant for species that depend on niche construction, a process whereby organisms, through their impacts on habitats or on other species, modify their own niche (Odling-Smee, Laland & Feldman 2003). In this case, as species' impacts will affect species' persistence only if these impacts influence, in turn, species' requirements, the need to distinguish species' impacts as a separate part of the niche is even less clear (Vázquez 2005).

Overall, drawing a firm distinction between each concept of niche and selecting one as being better than others seems neither necessary nor useful. In fact, given the great inherent flexibility of the concept of ecological niche, we believe that searching for a definitive definition and a unique metric of ecological specialization is probably meaningless. An alternative approach is to popularize major strengths and weaknesses of using definitions and/or metrics of ecological specialization to allow their best use in applied problems.

Interestingly, despite the limitations mentioned above, we have shown that most studies have explicitly or implicitly distinguished species' requirements from species' impacts when measuring specialization (with or without explicit reference to



Grinnell, Elton or to any conception of the niche) and as a species-specific attribute (i.e. fundamental) or as dependent on particular environmental conditions (i.e. realized). Therefore, the distinction between classical facets of the ecological niche (Eltonian and Grinnellian vs. fundamental and realized) still remains a practical heuristic basis which is flexible enough to embrace most concepts and metrics linked to specialization while discriminating different objectives (Fig. 4).

#### OTHER USEFUL APPROACHES FOR MEASURING ECOLOGICAL SPECIALIZATION

As emphasized in this review, the concept of specialization and its related metrics could be further defined according to narrower distinctions useful for different applied investigations. For instance, Ferry-Graham *et al.* (2002) proposed that functional specialization (driven by morphological traits) could be distinguished from behavioural specialization (a species whose behaviour allows capturing specific items among a pool of prey items available). This distinction can be used to assess different management efforts targeting species with specific roles because of their functional traits or behaviour. Following our framework, these two types of specialization can be classified as Eltonian specialization (the breadth of impacts). Similarly, food-resource specialization and habitat-specialization may further be differentiated as two aspects of Grinnellian specialization for specific management targets when needed (see e.g. Hughes 2000; Silvertown *et al.* 2006).

Alternatively, specialization can be measured independently of any firm distinction between Grinnellian and Eltonian niche. For instance, Fridley *et al.* (2007) have recently proposed that measurement of ecological specialization can be based upon the assumption that generalist species should co-occur with many different species across sites, whereas specialists should co-occur with relatively few species. This attribute can be easily quantified from species' co-occurrence patterns. This metric indirectly quantifies the Grinnellian realized specialization as it reflects the species' response (in terms of occurrence) to environmental heterogeneity (which is embodied by the diversity of co-occurring species). This measure also implicitly incorporates each species' impact on each other (as co-occurrence patterns are shaped by biotic interactions). As such, this metric also indirectly reflects Eltonian realized specialization (the capacity to interact with few or many species).

More generally, the distinction between realized vs. fundamental and Grinnellian vs. Eltonian niche is far from offering a complete typology of the ecological niche. Other concepts, more or less related to historical developments of the niche concept have also been proposed (e.g. niche construction, Odling-Smee *et al.* 2003; ecological versatility, MacNally 1995). Moreover, the distinction between fundamental and realized niche has mainly been influenced by the view that interspecific competition was the major driving force of community structure and composition. This limitation has prevented authors using Hutchinson niche from considering other interspecific interactions.

Recently, Vázquez (2005) has proposed a refinement of the Hutchinson niche to differentiate between (1) the multidimensional fundamental niche, corresponding to the environmental space delineated by all biotic and abiotic environmental factors within which the species can maintain viable populations. Only some combinations of these environmental factors are realized at a given point in space and time, which correspond to the realized environmental space (Jackson & Overpeck 2000). (2) The realized niche is the portion of the realized environmental space in which the populations actually exist in the field. (3) Finally, the portion of this realized environmental space in which individuals are not present (but could survive and reproduce) is the potential niche. The difference between the realized and the potential niche is thus contingent to source-sink dynamics, demographical stochasticity and dispersal constraints.

In this latter approach, the major difference between fundamental and realized niches compared to the classical Hutchinsonian distinctions is that fundamental specialization incorporates other species and is only conditioned on the ability of species to survive. The great advantage of these extensions to traditional definitions is that they correspond to more realistic situations encountered in applied ecology. Overall, we suggest that any metric of ecological specialization should be accompanied with a well-defined conception of the niche. Indeed, the use of ecological niche and specialization is not a problem *per se* but confusions often rise from the mismatch between the data used, the theoretical assumptions and the question being addressed.

#### MANAGEMENT IMPLICATIONS AND FUTURE RESEARCH DIRECTIONS

Once Grinnellian and Eltonian niche breadth are identified as two different aspects of ecological specialization, one may ask whether Eltonian and Grinnellian specialization can be measured independently. More generally, investigating whether and how different facets of ecological specialization are related to each other should provide considerable insight into several theoretical or conservation management issues.

First, the distinction between Grinnellian vs. Eltonian specialization should facilitate to investigate the so-called *biotic homogenization process*. According to this process, human-induced environmental and climate changes act as non-random filters, selecting species best able to survive within modified ecosystems. Despite the increasing use of the term biotic homogenization in conservation biology, practical means to measure this process are still largely missing and the underlying ecological mechanisms involved remain unclear. While growing evidence suggests that Grinnellian generalists tend to replace Grinnellian specialists following habitat degradation (Devictor *et al.* 2008), whether this process is different when using Eltonian specialization is unknown. This issue is a matter of considerable conservation interest as the loss of specific functions (i.e. performed by Eltonian specialists) can eventually lead to the loss of ecological interactions and processes with important consequences at the ecosystem level (Clavel, Julliard & Devictor, in press).

Secondly, the consequences of scale-dependence of realized vs. fundamental specialization remain poorly understood in conservation biogeography so that species are most often considered to be equally specialized across spatial scales. For instance, macroecological theory predicts that fundamental Grinnellian specialists should have smaller geographical range than Grinnellian generalists (the so-called Brown hypothesis, Brown 1984). Yet, Grinnellian specialists which are geographically rare, and therefore extinction-prone species, are also more likely to persist if they adopt a generalist strategy locally (Williams *et al.* 2006). Recognizing the spatial and temporal dimensions of the niche will also facilitate to re-frame different applied problems. For instance, observed colonization events of a specialist species can result from new occupations of its potential niche, from a true shift in its fundamental niche or from rapid changes in the realized environment. In each case, management implications (e.g. to reinforce or control the population increase) would be different. In particular, management options can shape the available potential niche at local and short-time scales (to increase or limit extensions of the realized niche) whereas halting a natural shift of the fundamental niche would need to consider management in accordance with evolutionary time scales.

Finally, acknowledging the difference between Eltonian and Grinnellian specialization can facilitate to formulate explicit objectives of conservation plans. For instance, conservation programmes focusing on the protection of a few individuals of an endangered species are more related to Grinnellian specialization (what individuals need to survive) while other programmes focusing on ecosystem functioning are more interested in Eltonian specialization (what specific functional roles are lost following the depletion of large populations).

## Concluding remarks

Although ecological specialization is a conceptual cornerstone in ecology, its definition is highly context-dependent and inconsistently used in applied ecology. In this study, we have shown how specialization is intrinsically linked to the niche concept, being nothing more than a measurement of a particular characteristic of the niche (the niche breadth). However, just as the niche is 'one of the most confusing, and yet important topics in ecology' (Root 1967), measuring ecological specialization has also created confusion in the literature, mostly because of the increasing diversity in the quantity and type of data available as well as in the scales considered. In integrating the classical Grinnellian/Eltonian and realized/fundamental axes underlying the niche concept, this review should facilitate to place most of applied measures of ecological specialization in their most appropriate empirical and theoretical use. By doing so, one should be more able to compare results of different studies and draw consistent conclusions on the impact of global changes on specialist vs. generalist species (Colles *et al.* 2009). Testing explicit predictions based on the different facets of ecological specialization should also open new avenues for the connection between biogeography, evolutionary and func-

tional ecology, one of the most pressing challenges for ecology and conservation.

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## References

- Ackerly, D.D. & Cornwell, W.K. (2007) A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. *Ecology Letters*, **10**, 135–145.
- Ashworth, L., Aguilar, R., Galetto, L. & Aizen, M.A. (2004) Why do pollination generalist and specialist plant species show similar reproductive susceptibility to habitat fragmentation? *Journal of Ecology*, **92**, 717–719.
- Austin, M.P., Nicholls, A.O. & Margules, C.R. (1990) Measurement of the realized qualitative niche: environmental niches of five Eucalyptus species. *Ecological Monograph*, **60**, 161–177.
- Bascompte, J., Jordano, P., Melián, C.J. & Olesen, J.M. (2003) The nested assembly of plant-animal mutualistic networks. *Proceedings of the National Academy of Sciences*, **100**, 9383–9387.
- Bearhop, S., Adams, C.E., Waldrons, S., Fuller, R.A. & Macleod, H. (2004) Determining trophic niche width: a novel approach using stable isotope analysis. *Journal of Animal Ecology*, **73**, 1007–1012.
- Bellwood, D.R., Wainwright, P.C., Fulton, C.J. & Hoey, A.S. (2006) Functional versatility supports coral reef biodiversity. *Proceedings of the Royal Society of London B*, **273**, 101–107.
- Blüthgen, N., Fründ, J., Vázquez, D.P. & Menzel, F. (2008) What do interaction network metrics tell us about specialization and biological traits? *Ecology*, **89**, 3387–3399.
- Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulseley, C.D. & Forrester, M.L. (2003) The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist*, **161**, 1–28.
- ter Braak, C.J.F. (1986) Canonical correspondence analysis: a new eigen-vector technique for multivariate direct gradient analysis. *Ecology*, **67**, 1167–1179.
- ter Braak, C.J.F. (1987) *Canoco – A Fortran Program for Canonical Community Ordination by Partial Detrended Canonical Correspondence Analysis and Redundancy Analysis*. Groep Landbouwwisgeving, Wageningen.
- Brown, J.H. (1984) On the relationship between abundance and distribution of species. *The American Naturalist*, **124**, 255–279.
- Calenge, C. & Basille, M. (2008) A general framework for the statistical exploration of the ecological niche. *Journal of Theoretical Biology*, **252**, 674–685.
- Carnes, B.A. & Slade, N.A. (1982) Some comments on niche analysis in canonical space. *Ecology*, **63**, 888–893.
- Chase, J.M. & Leibold, M.A. (2003) *Ecological Niches: Linking Classical and Contemporary Approaches*. University of Chicago Press, Chicago, IL.
- Clavel, J., Julliard, R. & Devictor, V. (in press) Worldwide decline of specialist species: towards a global functional homogenization? *Frontiers in Ecology and Environment*.
- Colles, A., Liow, L.H. & Prinzing, A. (2009) Are specialists at risk under environmental change? Neocological, paleoecological and phylogenetic approaches. *Ecology Letters*, **12**, 849–863.
- Colwell, R.K. & Futuyma, D.J. (1971) On the measurement of niche breadth and overlap. *Ecology*, **52**, 567–576.
- Devictor, V. & Robert, A. (2009) Measuring community responses to large-scale disturbance in conservation biogeography. *Diversity and Distribution*, **15**, 122–130.
- Devictor, V., Julliard, R., Clavel, J., Jiguet, F., Lee, A. & Couvet, D. (2008) Functional biotic homogenization of bird communities in disturbed landscapes. *Global Ecology and Biogeography*, **17**, 252–261.

- Dolédéc, S., Chessel, D. & Gimaret-Carpentier, C. (2000) Niche separation in community analysis: a new method. *Ecology*, **81**, 2914–2927.
- Dunne, J.A., Williams, R.J. & Martinez, N.D. (2002) Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters*, **5**, 558–567.
- Elton, C. (1927) *Animal Ecology*. Sidgwick and Jackson, London.
- Engelmann, K.E. & Schlichting, C.D. (2005) Coarse- versus fine-grained water stress in *Arabidopsis thaliana* (Brassicaceae). *American Journal of Botany*, **92**, 101–106.
- Feinsinger, P., Spears, E.E. & Poole, R.W. (1981) A simple measure of niche breadth. *Ecology*, **62**, 27–32.
- Ferry-Graham, L.A., Bolnick, D.I. & Wainwright, P.C. (2002) Using functional morphology to examine the ecology and evolution of specialization. *Integrative and Comparative Biology*, **42**, 265–277.
- Fridley, J.D., Vandermaast, D.B., Kuppinger, D.M., Manthey, M. & Peet, R.K. (2007) Co-occurrence based assessment of habitat generalists and specialists: a new measurement of niche width. *Journal of Ecology*, **95**, 707–722.
- Futuyma, D.J. & Moreno, G. (1988) The evolution of ecological specialisation. *Annual Review of Ecology and Systematics*, **19**, 207–233.
- Gregory, R.D., van Strien, A., Vorisek, P., Meyling, A.W.G., Noble, D.G., Foppen, R.P.B. & Gibbons, D.W. (2005) Developing indicators for European birds. *Philosophical Transactions of the Royal Society B*, **360**, 269–288.
- Grinnell, J. (1917) ‘The niche relationship of the California Thrasher’. *The Auk*, **34**, 427–433.
- Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8**, 993–1009.
- Hughes, J.B. (2000) The scale of resource specialization and the distribution and abundance of lycaenid butterflies. *Oecologia*, **123**, 375–383.
- Hutchinson, G.E. (1957) Concluding remarks. Cold Spring Harbor Symposium. *Quantitative Biology*, **22**, 415–427.
- Jackson, S.T. & Overpeck, J.T. (2000) Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology*, **26**, 194–220.
- Julliard, R., Clavel, J., Devictor, V., Jiguet, F. & Couvet, D. (2006) Spatial segregation of specialists and generalists in bird communities. *Ecology Letters*, **9**, 1237–1244.
- Kassen, R. (2002) The experimental evolution of specialists, generalists, and the maintenance of diversity. *Journal of Evolutionary Biology*, **15**, 173–190.
- Kearney, M. (2006) Habitat, environment and niche: what are we modelling? *Oikos*, **115**, 186–191.
- Kearney, M. & Porter, W.P. (2004) Mapping the fundamental niche: physiology, climate and the distribution of nocturnal lizards across Australia. *Ecology*, **85**, 3119–3131.
- Krasnov, B.R., Mouillot, D., Khokhlova, I.S., Shenbrot, G.I. & Poulin, R. (2008) Scale-invariance of niche breadth in fleas parasitic on small mammals. *Ecography*, **31**, 630–635.
- 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.
- Levins, R. (1968) *Evolution in Changing Environments*. Princeton University Press, Princeton, NJ.
- MacArthur, R.H. (1972) *Geographical Ecology*. Harper & Row, New York, NY.
- McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, **21**, 178–185.
- McKinney, M.L. (1997) Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annual Review of Ecology and Systematics*, **28**, 495–516.
- MacNally, R.C. (1995) *Ecological Versatility and Community Ecology*. Cambridge University Press, Cambridge.
- Milesi, F.A. & López de Casenave, J. (2005) El concepto de nicho en Ecología Aplicada: del nicho al hecho hay mucho trecho. *Ecología Austral*, **15**, 131–148.
- Mouillot, D., Mason, N.W.H. & Wilson, J.B. (2007) Is the abundance of species determined by their functional traits? A new method with a test using plant communities. *Oecologia*, **152**, 729–737.
- Odling-Smee, F.J., Laland, K.N. & Feldman, M.W. (2003) *Niche Construction: The Neglected Process in Evolution*. Princeton University Press, Princeton, NJ.
- Pickett, S.T.A. & Bazzaz, F.A. (1978) Organization of an assemblage of early successional species on a soil moisture gradient. *Ecology*, **59**, 1248–1255.
- Pulliam, R. (2000) On the relationship between niche and distribution. *Ecology Letters*, **3**, 349–361.
- Root, R.B. (1967) The niche exploitation pattern of the blue-gray gnatcatcher. *Ecological Monograph*, **37**, 317–350.
- Rosenfeld, J.S. (2002) Functional redundancy in ecology and conservation. *Oikos*, **98**, 156–162.
- Roughgarden, J. (1972) Evolution of niche width. *The American Naturalist*, **106**, 683–718.
- Sargeant, B.L. (2007) Individual foraging specialization: niche width versus niche overlap. *Oikos*, **116**, 1431–1437.
- Silvertown, J., Dodd, M., Gowing, D., Lawson, C. & McConway, K. (2006) Phylogeny and the hierarchical organization of plant diversity. *Ecology*, **87**, 39–49.
- Smith, E.P. (1982) Niche breadth, resource availability, and inference. *Ecology*, **63**, 1675–1681.
- Soberón, J. (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, **10**, 1115–1123.
- Thomson, J.D., Weiblen, G., Thomson, B.A., Alfaro, S. & Legendre, P. (1996) Untangling multiple factors in spatial distributions: lilies, gophers, and rocks. *Ecology*, **77**, 1698–1715.
- Thuiller, W., Lavorel, S. & Araújo, M.B. (2005) Niche properties and geographical extent as predictors of species sensitivity to climate change. *Global Ecology and Biogeography*, **14**, 347–357.
- Vázquez, D.P. (2005) Reconsiderando el nicho hutchinsoniano. *Ecología Austral*, **15**, 149–158.
- Venail, P., MacLean, R.C., Bouvier, T., Brockhurst, M.A., Hochberg, M.E. & Mouquet, N. (2008) Functional diversity and productivity peak at intermediate levels of dispersal in evolving metacommunities. *Nature*, **452**, 210–215.
- Williams, Y., Williams, S.E., Alford, R.A., Waycott, M. & Johnson, C.N. (2006) Niche breadth and geographical range: ecological compensation for geographical rarity in rainforest frogs. *Biology Letters*, **2**, 532–535.
- Winemiller, O. & Pianka, E.R. (1990) Organization in natural assemblages of desert lizards and tropical fishes. *Ecological Monographs*, **60**, 27–55.
- Wright, J.W., Davies, K.F., Lau, J.A., McCall, A.C. & McKay, J.K. (2006) Experimental verification of ecological niche modeling in a heterogeneous environment. *Ecology*, **87**, 2433–2439.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Fig. S1.** Two classical approaches to measure Grinnellian and Eltonian specialization.

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