

The hutchinsonian and eltonian shortfalls



**ASSIGN
BUSTER**

A number of recognized knowledge shortfalls currently exist in biology. The first that appears to have been identified is taxonomical, and is known as the Linnean shortfall (Raven and Wilson, 1992). This concerns the disparity between species described by scientists and the actual number of species in the world. The second, the Wallacean shortfall, is biogeographical, and is related to uncertainties in the geographical distribution of species (Lomolino 2004). The Prestonian deficit is related to the scarcity of species abundance data (Cardoso et al. 2011), and the Darwinian shortfall is related to the lack of evolutionary data, such as phylogenies, uncertainties in phylogenies already available, and lack of understanding of convergence and conservatism of functional traits (Diniz-Filho et al. 2013). The fifth and final shortfall is the Hutchinsonian, which is related to uncertainty regarding the functional roles of species and their habitat requirements (Cardoso et al. 2011).

Hutchinson (1957) proposed an important milestone in ecology: the quantitative approach to describing an environmental niche, defined as an n-dimensional hypervolume of factors that limit where a species could occur. However, Hutchinson's niche definition does not differ substantially from the Grinnellian view, which is focused on species' requirements but not on the effect of species on a given habitat, as considered by Charles Elton (Chase and Leibold 2003). This distinction between the concepts of niche hinges on the different spatial scales in which they operate. The Grinnellian niche applies to broad scales (the so-called beta niche), where the occurrence of a given species is related to its abiotic requirements (i. e. physiological niche or fundamental niche). The Eltonian niche, however, concerns the local scale

and reflects the realized niche of a species, because it considers physiological tolerances and biotic interactions (Ackerly 2003, Soberón 2007). In this sense, the Hutchinsonian shortfall may be decomposed into the Eltonian shortfall. This term is used to refer to our lack of knowledge regarding intra- and interspecific interactions (Peterson et al. 2011) and the effects of species on ecosystems.

For our purposes it is important to recognize the dichotomy between the Grinnellian and Eltonian concepts of niche, as habitat and as function respectively, and how understanding these differences may help ecologists to fill the Eltonian gap in our knowledge. Although Cardoso et al. (2011) have suggested ways to solve the Hutchinsonian shortfall, and explore its relationship with some of the other shortfalls, focused on biological conservation (Cardoso et al. 2011), no theoretical framework for how to deal with these problems has yet been proposed. Hence, before we can make progress in practical issues such as conservation, we first need to improve our theoretical framework so that we can appropriately address any research field in ecology (Marquet et al. 2014).

This dichotomy in niche concepts, as already argued from a geographical perspective (Soberón 2007), may underlie the problem of using functional traits, chosen based on large-scale datasets, to address local questions (Cordlandwehr et al. 2013, Rosado et al. 2013). The importance of careful choice of functional traits when using them as proxies for ecological processes has been highlighted repeatedly (Díaz et al. 2002, Lavorel et al. 2013, Rosado et al. 2013). However, we argue that the functional approach, which emerges from niche theory (Leibold 1995, McGill et al. 2006, Westoby

<https://assignbuster.com/the-hutchinsonian-and-eltonian-shortfalls/>

and Wright 2006), has neglected the dichotomy between the Grinnellian and Eltonian concepts of niche. Here, we explore how scientists working with the functional approach must be circumspect about choice of functional traits, and should be aware of the implicit problems in the following question: Do we know enough about the biology of species and their local populations to identify the important traits, assuming niche as habitat (species requirements) and/or niche as function (role of species), to address a given question (e. g. what are the processes behind community assembly, how will species respond to environmental pressures such as deforestation, and how do we plan systematic planning for conservation)?

Here, we present a theoretical framework that explores the Hutchinsonian and Eltonian shortfalls in depth (Fig. 1). We present the main gaps in current knowledge, problems and caveats of which researchers should be aware, and possible solutions that might enable us to move forward.

The common approach: the Grinnellian view

In the recent past, the effect of functional traits on community assembly and the resistance/resilience of communities, and consequently on ecosystem functioning, has been one of the most prominent lines of investigation in ecological research (Rees et al. 2001, Sutherland et al. 2013, Tilman et al. 1997). Recently, advances have been made in the description of the functional role of species in food webs, community structure and ecosystem processes (Araújo et al. 2011, Lavorel and Garnier 2002, Wiens et al. 2010). This functional-based approach relies on the ecological significance of functional traits, such as specific leaf area and body size, which may be used

as proxies to describe ecological processes at community and ecosystem levels. Although this topic has recently been included as one of the 100 fundamental questions of ecology (Sutherland et al. 2013), important constraints may arise because the ecological significance of functional traits, commonly chosen based on global datasets, may not apply at local scales (Díaz et al. 2002, Rosado et al. 2013). These limitations arise, for instance, due to plasticity in traits and differences and at different stress levels in a given environment, which lead to varying ecological significance of traits (Cordlandwehr et al. 2013). The existence of such large datasets does not, therefore, warrant their use for research being conducted at local scales.

As pointed out by Sóberon (2007), although the distinction of niche as habitat and niche as function has already been made, the distinction of niche between large and small scales and the changes in the ecological significance of functional traits across scales is rarely considered. This distinction is especially important given that functionally different species coexist at broad scales (i. e. the Grinnellian niche concept) (Ackerly 2003). Even when this is the case, however, their niches and interactions at local scales depend on their competitive abilities. Therefore, traits that may predict potential distribution and coexistence at broad scales (fundamental niche) do not necessarily explain how species coexist at local scales (realized niche) or their effects on community assembly (Fig. 1). Interestingly, McGill et al. (2006) previously raised these questions and suggested that researchers go beyond “ What are the most important niche dimensions? To ask what traits are most decisive in translating from fundamental niche to

realized niche?” However, to our knowledge, there are as yet no published studies on this issue.

Traits to answer questions on community assembly and ecosystem functioning are frequently selected based on their availability in global datasets (Jones et al. 2009, Kattge et al. 2011, Wright et al. 2004). However, this seems to ignore recent advances in community phylogenetics that allow one to assess the degree of phylogenetic signal imprinted on traits (Blomberg et al. 2003, Webb et al. 2008) and, therefore, the phylogenetic conservatism of niches (Crisp and Cook 2012). High phylogenetic conservatism of traits has been observed at broad scales, which indicates a Grinnellian conservatism of niche (Soberón 2007). At local spatial scales, therefore, choice of traits must take into account the effects of ecological processes that operate at those scales (Ackerly, 2003). However, evidence of niche conservatism in Eltonian niches (i. e. local scales) is lacking (Soberón 2007), especially considering that most functional traits used in studies (e. g. body size, life history, specific leaf area) may be highly conserved (Ackerly 2003, Blomberg et al. 2003, Crisp and Cook 2012, Soberón 2007). Even if phylogenetic conservatism of traits is taken into account when the niche breadth of species is evaluated, it is constrained to the physiological dimension at broad scales (i. e. Grinnellian niche) (Gouveia et al. 2013) and does not consider the functional role of species at local scales.

Unifying niche concepts: response and effect

Although a concept of niche that would unify the Eltonian and Grinnellian views was proposed 10 years ago by Chase and Leibold (2003), it seems that

the dichotomy remains, especially regarding the choice of functional traits and concepts of niche used at different spatial scales (Godsoe 2010, Kearney et al. 2010, McGill et al. 2006). This idea has been explored from a geographic perspective, mainly in the context of niche modeling (Soberón 2007, Peterson and Soberón 2012), but these analyses used only climatic and topographic variables. Based on a consumer-resource model developed by MacArthur (1972), Tilman (1982) proposed the resource-ratio theory. This theory is based on the idea of R^* , which is defined as the concentration of available resources that a species requires to survive in a habitat, and was later improved by Chase and Leibold (2002). In the original model, R^* describes the resource level required for a species to reach a zero net growth isocline (Grinnellian approach), The model also predicts that species with the lowest R^* are able to displace all competitors whose R^* is higher (Eltonian approach) (Tilman, D. 1990). Chase and Leibold (2003) included not only the dimension of resource-use (R^*), but also tolerance to stress (S^*) and predators (P^*), to better describe a species' niches in terms of both its requirements (sensu Grinnell) and its effects on the environment, e. g. changes in resource availability and density of predators (sensu Elton) (Chase and Leibold 2003).

Looking ahead

Although there has been an effort to identify studies supporting Tilman's theory (Miller et al. 2005, Wilson et al. 2007), there are few studies that identify functional traits that can be used as proxies for R^* (Fargione and Tilman 2006, Jabot and Pottier 2012), especially in relation to the other niche dimensions (S^* and P^*) (Kearney et al. 2010). Interestingly, the interplay

<https://assignbuster.com/the-hutchinsonian-and-eltonian-shortfalls/>

among R^* , S^* and P^* has been explored in the search for functional traits as proxies for niche requirements, not the functional role of species (Chase and Leibold. 2003, Kearney et al. 2010). A correlation between “ response traits” and “ effect traits” affecting ecosystem functioning and service delivery has been identified (Lavorel 2013, Lavorel and Garnier 2002, Lavorel et al. 2013). Despite this, a trait-based approach describing the effect of a species on interaction networks, reflected by the interplay among R^* , S^* and P^* (Chase and Leibold 2003), is still lacking. Only recently has a combination of trait-based approaches and interaction networks been formulated to cover the functional relationships of trophic interactions, although this only focuses on ecosystem services (Lavorel, S. et al. 2013). It does, however, take into account the distinction between response and effect traits.

While difficulties associated with the use of traits at different scales appear to have been overlooked, substantially more effort has been spent in the development of analytical tools to characterize functional diversity using different indices (Lavorel et al. 2008, Lepš et al. 2006, Mouchet et al. 2010, Pillar et al. 2009, Schleuter et al. 2010, Villéger et al. 2008). We do not intend to argue against this focus on advancing our analytical tools, but we suggest directing more attention to the prior step. Before deciding which functional diversity indices to use (Schleuter, D. et al. 2010), we need to define not only which traits should be chosen to feed the indices (Rosado et al. 2013), but also whether those traits fit the niche perspective being used. Recently, Hille Ris Lambers et al. (2012) proposed that community assembly studies focusing on processes leading to competitive exclusion and coexistence should combine trait-based approaches to demographic

analysis, based on Tilman's model. Taking into account that the impact of a species may also be described by trait-based approaches and demographic analysis, we propose that a better description of Eltonian niches may also be achieved by merging effect traits into Tilman's model. Additionally, the correct identification of response and/or effect traits (Lavorel et al. 2013) is extremely important in the interplay between R^* , S^* and P^* . Although the resource-ratio theory may be viewed as an inefficient theory because of the difficulty of testing it (for more details see Marquet et al. 2014), we believe that our framework (Fig. 1) also has a heuristic value (Marquet et al. 2014). Our framework may provide ecologists with a useful conceptual basis, and aid in the choice of traits with respect to niche concepts and in selecting possible tools for dealing with the Eltonian shortfall.

In conclusion, although Wiens (1989) has pointed out that understanding the "drama in the ecological theater" (Hutchinson 1965) depends on scale, it seems that a functional approach needs to return to basics with respect to how the two niche perspectives (responses vs. effect) should be applied at different scales (Chase and Myers 2011). Otherwise, there can be no understanding of the processes behind community assembly and species distributions. A reasonable idea of how to model a species niche as a response (species requirements) now exists, but the problem of identifying which traits are ecologically relevant, and how to measure them properly, remains. This, therefore, is the "Eltonian shortfall" of knowledge and one of the most important current challenges in the study of ecology.