

# Trait-based plant ecology: moving towards a unifying species coexistence theory

## Features of the Special Section

Adrián Escudero<sup>1</sup> · Fernando Valladares<sup>1,2</sup>

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**Abstract** Functional traits are the center of recent attempts to unify key ecological theories on species coexistence and assembling in populations and communities. While the plethora of studies on the role of functional traits to explain patterns and dynamics of communities has rendered a complex picture due to the idiosyncrasies of each study system and approach, there is increasing evidence on their actual relevance when aspects such as different spatial scales, intraspecific variability and demography are considered.

We are witnessing an impressive development of what has been called “functional plant ecology” (Violle et al. 2007). This discipline is based on the simple idea that plants affect the functioning of communities and ecosystems through their morphological and physiological attributes, i.e., through their traits. As discussed in depth in this special section, the very term “functional ecology” is ambiguous and needs to be re-phrased as “trait-based ecology” (Shipley et al. 2016). The exponential increase in the number of research efforts on this topic over the past decade is due to the rediscovery of one of the most ancient debates in the discipline of ecology: what are the drivers of plant species

coexistence (HilleRisLambers et al. 2012; Götzenberger et al. 2012), as provocatively put by Ricklefs (2008): do plant communities exist as discrete entities or not? [See also the reply of Brooker et al. (2009).]

Since the early development of plant ecological theory (Clements 1916; Gleason 1926), this debate has moved back and forth between invocation of the ultimate roles of deterministic versus stochastic mechanisms (Wilson 1990; Vellend et al. 2014). These shifting discussions can be paradigmatically exemplified at one extreme by the preponderance of the so-called assembly rules (Diamond 1975), deeply rooted in the existence of different Hutchinsonian niches among species. At the other extreme is the dominance stochastic processes under what has often been described as “ecological neutrality” (Hubbell 2001). The history of debate on this question of the mechanisms that promote plant coexistence constitutes a never-ending spiral in which concepts are posited, only to be forgotten later and once again rediscovered or redefined. For example, the importance of stochasticity, which emerged principally from the seminal paper of Hubbell (2001), can be traced with other names to the so-called ‘equal chance’ concept of Connell (1978) or the ideas of the ‘good fortune’ concept of Fagerström (1988), and the development of different lottery models in the work of Shmida and Ellner (1984).

In an attempt to delimit this topic of plant coexistence and to unveil all its facets, functional plant ecology or, better stated, plant trait-based ecology, has emerged as a powerful conceptual and operative tool (Shipley et al. 2016).

In its detail, plant trait-based ecology rests on a foundation of plant functional traits from individuals to communities, and the role of these traits in shaping consensus responses to past and present ecological selective pressures, whether abiotic, biotic or both (Westoby et al. 2002). In its most classic perspective, the different ecological roles of

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✉ Fernando Valladares  
valladares@cma.csic.es

<sup>1</sup> Área Biodiversidad y Conservación, Departamento de Biología y Geología, ESCET, Universidad Rey Juan Carlos, 28933 Móstoles, Madrid, Spain

<sup>2</sup> LINCGlobal, Department of Biogeography and Global Change, National Museum of Natural History, MNCN, CSIC, Serrano 115 bis, 28006 Madrid, Spain

each species and individual are related to morphological, physiological, behavioral and phenological features affecting fitness and persistence through time (Cadotte et al. 2011), reducing competition and promoting specialization (Kraft et al. 2015). Plant trait-based ecology can be connected to theories on ecological niche and its role in determining competitive interactions (Hutchinson 1957), ecological assembly rules (Diamond 1975) and ecological filters (Keddy 1992). These filters can be of a very different nature (abiotic or biotic), can be related to dispersal (Götzenberger et al. 2012), and can be probabilistic or not, with traits having contrasting probabilities of passing through the “environmental sieve” (Shipley 2010). In turn, trait-based ecology provides a mechanistic connection between ecological processes and these deterministic processes (Weiher and Keddy 1995; Westoby and Wright 2006; McGill et al. 2006). From our perspective, the stochastic versus deterministic notions constitute complementary and not mutually exclusive aspects of a very complex process (Gravel et al. 2006), and their relative importance varies across biomes and ecological conditions (Valladares et al. 2015).

The collection of papers in this special issue provides a broad basis for understanding the contrasting study cases that have fueled past debate, sometimes acrimonious, on the form and relevance of plant trait-based ecology. As commented by Götzenberger et al. (2012), we are far from completing the picture of the processes that govern plant species coexistence, be they deterministic or stochastic. Integration of all these positions can be done by improving the theoretical background of Plant Trait-based Ecology, by simplifying the labyrinth of functional metrics (de Bello et al. 2016) and by facing some of the most ancient questions of the discipline from different perspectives.

Here, we have designed a road map to the perspectives represented in this section.

## A demographic perspective

Probably one of the most demanding requirements to understand species coexistence is to better connect plant trait configuration with the viability and persistence of individual populations. Such a necessity implies the need to view the plant community not at one instant in time—the realized assemblage—but as a shifting set of assemblages, in which some populations are expanding and others are shrinking. It is critical in this context to understand that species’ traits differentially affect various aspects of assemblage shifts, affecting the entire life cycle of individuals such as fertility, migration, growth and survival [response traits sensu Violle et al. (2007)]. In other words, plant trait-based ecology must incorporate a demographic

perspective. As discussed in the contribution of Shipley et al. (2016), the main impediment to improving this demographic framework is the measurement of plant population parameters for many different species in many different environments. This demographic framework comes from the historical work conducted by plant population ecologists (Harper 1977) and it is also related to the so-called emergent/contemporary/modern coexistence theory (HilleRisLambers et al. 2012) based on the influential work of Chesson (2000). This school recognizes that the niche describes all aspects of species interactions with their environment and their associated competitive outcomes (Godoy et al. 2014). They introduce two complementary concepts that consider all possible plant–plant interactions under a given local environment: stabilizing niche differences, and average fitness differences (HilleRisLambers et al. 2012).

Recently, Kraft et al. (2015) made a titanic effort to characterize field-measured life stage parameters and pairwise competitive interaction coefficients of a small experimental guild of annuals formed by 18 species in order to estimate their niche and fitness differences. Such efforts are not feasible in most cases and are not free of important limitations. Here, Lloret et al. (2016) propose an easier procedure to infer demographic trends by measuring differences in cover after an extreme climate-driven die-off. These demographic performance estimates were related to plant trait configurations as a step to predict community assembly outcomes following critical climate events.

## An individual’s perspective

Discrepancies among papers on the topic of coexistence often arise as a consequence of differences in the spatial scales considered. If plant interactions at fine scales are truly mediated by interspecific trait differences they must leave a strong spatial signal not only in the taxonomic profile but also in the functional structure of the community. Our recommendation in this context is to introduce the perspective of individuals (sensu Murrell et al. 2001) and to simultaneously survey a complete set of scales (see Wiegand and Moloney 2004). This quantification and integration would unveil whether the observed patterns are related to the plant trait structure of the community or not. In the paper of Chacón-Labelle et al. (2016) some species showed a high capacity to affect the spatial structure of specific functional traits, but this capacity was restricted to the finest spatial scales. The patterns found suggested the prevalence of two processes controlling the functional structure of the community at fine scales: biotic filtering, and resource partitioning controlled by an indirect facilitation mechanism.

## Intraspecific trait variability

Traditionally functional variability of plants has been collapsed at the species level by using the mean value. However, intraspecific trait variation (ITV) has been shown to be critical for responding to key questions in community ecology (Bolnick et al. 2011; Violle et al. 2012). In a recent meta-analysis (Siefert et al. 2015), ITV was evaluated and recommended for use in trait-based community ecology due to its importance, i.e., representing 25 % of the total trait variation, and extent, i.e., higher in whole plant traits and in regional studies. Volf et al. (2016) evaluated these two components as a response to disturbances of different intensity in meadows. Shifting environmental conditions lead to either changing species—presence/absence dichotomy—or modulating traits by adjusting, in turn, the relative abundance of some species, which is key to understanding how communities can respond to ongoing environmental change (Jung et al. 2014). An important source of intraspecific trait variability that can significantly contribute to this balance is phenotypic plasticity (Valladares et al. 2014).

Another critical aspect regarding ITV that needs attention is its variability over time. For instance, intraspecific phenological variation in key leaf traits was as great as interspecific variation in the comparative study, as commented on in detail in this section by Fajardo and Siefert (2016).

## Scaling up the functional approach

A potentially informative exercise is to scale up the trait-based approach to emergent interaction networks and to other surrogates of ecosystem structure. How these networks function in highly diverse communities is of increasing interest (Ings et al. 2009). Ibanez et al. (2016) studied the phylogenetic signal of some new network-level metrics (the taxonomic niche which is simply the identity of the interacting species) in comparison with the functional niche.

## Addressing the services provided by ecosystems

To establish a clear connection between trait-based theories and ecosystem services is a priority in the field of plant trait-based ecology because traits provide one of the most efficient tools for connecting diversity with the mechanistic process delivering ecosystem functions for humanity. This was the aim of Lavorel et al. (2016) by studying the potential ecological intensification of livestock production in the Alps. They explored the relationships between soil features, plant traits and management characteristics, and

found a connection between traits and management intensification, which is especially effective as a means to explain the variation of ecosystem goods and services. These variations agreed well with expectations from the leaf economics spectrum model and have important implications for understanding ecosystem functioning (see Cadotte et al. 2011).

## Final remarks

In summary, this special section is intended to provide insight into recent developments in how trait-based knowledge has emerged as a potential unifying framework within which key ecological theories can be organized concerning species coexistence and assemblage in populations and communities. This collection of papers cannot provide a complete picture of this topic and its unifying potential. However, we tried to assemble papers in some key areas with the hope of catalyzing further discussion and the development of new ideas. While the plethora of studies on the role of functional traits in explaining patterns and dynamics of communities has rendered a complex picture due to the idiosyncrasies of each study system and approach, there is increasing evidence of foundational concepts that are relevant and applicable to a broad range of ecological challenges that have emerged in the past decade. As editors of this section, we were pleased to see the energy and novelty of thought expressed by the contributors. We hope that readers will also recognize the benefit of these contributions.

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