

Biotic controls of plant coexistence

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Abstract:

1. The quest for understanding the maintenance of species diversity has matured in recent decades under the umbrella of species coexistence theory, founded by Chesson (2000). One central gist of the theory points out that coexistence between species at local scales depends on two opposing forces: average fitness differences between species, which drive the best-adapted species to exclude others, and stabilizing mechanisms, which promote diversity via niche differentiation.
2. One pressing aim which is gaining momentum is understanding how interactions of plant species with other organisms shape the maintenance of plant diversity by acting upon equalizing and stabilizing forces. But this interest contrasts with the lack of empirical information. Therefore, a fundamental step now is assessing the prevalence of these mechanisms on controlling plant coexistence across a wide range of interactions and systems.
3. To that end, this special feature presents 10 theoretical, observational or manipulative studies illustrating 9 different biotic interactions including mutualisms (pollinators, seed dispersers, soil microbes and arbuscular mycorrhizal fungi) and antagonisms (leaf and seed herbivores, and leaf and root pathogens). All studies share a common question ¿how biotic interactions regulate plant coexistence?
4. Comparisons across studies suggest that biotic interactions modify both niche and average fitness differences. In those cases where biotic interactions promote stable coexistence between plant species, both mutualistic and antagonistic interactions act more frequently as an equalizing rather than as a stabilizing mechanism.
5. Besides these generalities, the studies of this special issue also present novel theoretical and empirical approaches to better understand the maintenance of species diversity over a wide variety of systems, environmental conditions, and organisms.

6. *Synthesis*: The studies presented here constitutes a solid base to empirically explore how mutualistic and antagonistic interactions act upon the determinants of plant species competition, and open novel paths for future research. Collectively, these advances will likely serve to pave the road for a better theoretical and empirical understanding on how biotic interactions control biodiversity.

Key words: niche, fitness, apparent competition, multitrophic interactions, mutualisms, antagonisms.

Introduction

Ecologists have long recognized the strong role that competition for resources have in determining species coexistence. According to the principle of competitive exclusion (Grinnell 1904), two species cannot coexist under the same constant environment if they compete for the same limiting resource. The pioneer Russian biologist Georgyi Gause (1934), was among the first to empirically validate this principle. Gause studied population dynamics of two *Paramecium* species in homogeneous environmental conditions and demonstrated that in the absence of environmental heterogeneity which would mitigate the effects of interspecific competition, one species inevitably outcompeted the other to extinction. Later on, Tilman (1982) formalized mathematically such principle under the definition of the R^* , which predicts that if multiple species are competing for a single limiting resource, then whichever species can survive at the lowest equilibrium resource level (i.e., the lowest R^*) can outcompete all other species.

With this principle in mind, ecologists have long sought to determine which are the conditions that prevent species to exclude one another. The work of Joseph Grinnell was again critical. Grinnell (1924) defined the concept of the niche to explain the differences between species in habitat preferences and behavioral adaptations that allow them to coexist. After a few decades of strong discussion of what is a species' niche, ecologists mostly agree with Hutchinson's (1957) definition, who introduced the idea that the niche of a species is a multi-dimensional hypervolume, each dimension representing a relevant environmental factor (e.g. temperature, precipitation, etc.). Robert MacArthur (1958) presented in his famous study on New England warblers one of the first examples of the critical role of niche differences and its multidimensional nature for maintaining species coexistence. He proposed that the apparent contradiction for why so many bird species with similar appearance and ecological traits coexist in boreal forest can be explained by differences in breeding and feeding behaviours within distinct spatial parts of coniferous trees. This pioner work together with many other posterior examples (e.g. Diamond 1975, Ricklefs and Travis 1980) set the basis to justify patterns of species co-occurrence as niche differences among species.

The competitive exclusion principle and the niche partitioning concept were two long standing ideas in ecology that were not properly linked together until Chesson (2000). Coexistence theory developed by Peter Chesson has provided a conceptual framework and a powerful set of mathematical toolboxes to understand that stable coexistence between species can be predicted by two opposing forces. These are average fitness differences which drive the best-

adapted species to exclude others, and niche differences which stabilize coexistence by limiting dominance when species become common. The gist of coexistence theory is that species can coexist by the joint effect of equalizing mechanisms (i.e. species tend to show similar fitness) and stabilizing mechanisms (i.e. species tend to be differentiated in their niche), and stable coexistence occur when niche differences overcome fitness differences.

Coexistence theory has focused historically on the determinants of species coexistence within a single trophic level. The focus of interest has been generally primary producers in both terrestrial and aquatic systems (Chase et al. 2002, Godoy et al. 2018). Particularly for plants, competition driven by abiotic conditions has been considered the main driver of plant coexistence, and therefore it has been extensively explored (Raynaud & Leadley 2004; Tilman et al. 2006; Craine & Dybzinski 2013; Hendriks et al. 2015). For instance, ecology textbooks commonly present differences in the species' ability to drawdown limiting resources such as nitrogen and phosphorous as a key example illustrating the importance of partitioning soil resources for maintaining species diversity (Tilman 1994). However, the effect of multitrophic interactions on plant coexistence such as those occurring between plants and other organisms including floral visitors, leaf and root pathogens, herbivores, mycorrhizal fungi or soil microbes have received comparatively much less attention in the past decades (Fitter 1977; Bastolla et al. 2009; Bagchi et al. 2014; Parker et al. 2015; Bennett et al. 2017). This is a surprising fact for two reasons. First, biotic interactions have been historically at the core of ecological thinking, and as emphasized by Darwin himself, the species "struggle for existence" is not just between organisms and the abiotic environment, but include species interactions such as competition, but also predation, parasitism or mutualistic interactions (Darwin 1859). Second, there is extensive past theoretical work showing that shared enemies (e.g. herbivores, pathogens) can indirectly modulate competitive interactions among plant species (Holt 1977, 1984) and the strength of these apparent effects can limit or promote species coexistence in the same way do competitive interactions for soil resources (Chesson and Kuang 2008).

Understanding empirically how biotic interactions shape equalizing and stabilizing forces at the community level is gaining momentum (Mordecai 2013, Lanuza et al. 2018). Obtaining such knowledge is key to further understand coexistence of multiple trophic levels simultaneously (Godoy et al. 2018). But rather than doing progress isolatedly in terms of studying particular interaction types and species systems, we believe the time is ripe for a collectively effort in order to assess the importance of these biotic interactions in determining the assembly of ecological communities. This special feature presents 9 empirical studies of a wide range of competitive, mutualistic and antagonistic interactions. All share a common question: How biotic factors regulate plant coexistence? By summarizing the results of studies including the biotic effects of plant competition, mutualistic interactions with pollinators, seed dispersers, soil biota or mycorrhizal fungi, and antagonist interactions with leaf and seed herbivores or pathogens, we aim to gauge our ability to predict which species interactions promote the maintenance of plant diversity, and perhaps more importantly, we aim to mechanistically understand how these interactions promote plant diversity through its effects on the determinants of competitive outcomes, niche and fitness differences.

Both mutualistic and antagonistic interactions can either promote or limit the maintenance of plant diversity.

Applying coexistence theory to understand the biotic effects on plant coexistence, leads us to have direct expectations that both mutualistic and antagonistic interactions can either promote or limit plant diversity. These expectations are clear from a theoretical and empirical perspectives for antagonistic interactions (Chesson and Kuang 2008), but the coexistence mechanisms by which occur these modifications remain yet unclear. Several papers in this special feature shows that antagonist interactions equalize fitness differences between species. Maron et al. (2018) show in perennial bunchgrass prairies that species with larger seeds are better competitor compared to species with smaller seeds because they present a suite of traits associated with an acquisitive strategy (greater plant height, lower C/N ratios and lower water use efficiency). However, this competitive advantage is offset by rodent seed predators, which preferentially eats the the larger-seeded, and superior plant competitors. Petry et al. (2018) show in annual Californian grasslands a very similar competition-defence trade-off driven by an ant species acting as a generalist seed predator. With another antagonist interaction, Parker and Gilbert (2018), show also that faster-growing clover species experienced greater fungal infection than co-occurring slower-growing clovers. However, the competition-defence trade-off is less clear in this study as the reduction in fitness was not higher in faster-growing than in slower-growing clover species. Conversely, contributions included in this special feature have found less evidences that antagonistic interactions promote niche differences between competing plant species. Part of this lack of information emerges from the difficulty to design specific experimental and observational studies for capturing such stabilizing effects. But even in those cases where this information was possible to obtain, they have not found that antagonist interactions mediate greater intraspecific competition at local scales compared to interspecific competition (Parker and Gilbert, 2018). Indeed, in addition to the direct effect of antagonistic interactions on promoting niche and fitness differences, a pertinent question to ask is whether such estimated modifications in the determinants of competitive outcomes are enough to maintain plant diversity. A rigorous response to this question can be found in Lanuza et al. (2018) and in this special feature in Petry et al. (2018), which both show that the equalizing effect of the multitrophic interactions is not enough to maintain diversity at the scale of plant interactions as the observed fitness differences are still greater than the observed niche differences. However, diversity can be maintained at larger scales because consumers have different consumption rates across different locations, and such differences in consumer pressures define changes in the identity of the superior competitor.

Less clear in the literature has been the thinking that mutualisms either promote or limit plant diversity. Because both organisms involved in such biotic interaction obtain a benefit, it has been traditionally thought that mutualistic interactions promote in general plant diversity by minimizing competition between plant species (i.e. increasing niche differences) and by increasing proportionally more the fitness of the non-dominant species compared to the common (i.e. equalizing fitness differences) (Bastolla et al. 2009, Pauw 2013). However, there are not theoretical limitations to think that mutualistic interactions have the possibility to promote competitive exclusion by increasing fitness of the superior competitor species as well as by

reducing niche differences due to sharing for instance pollinators or mycorrhizal fungi. Indeed, studies included in this special feature found empirical support for both options, plant coexistence and competitive exclusion, but the mechanisms by which both outcomes occurred varied greatly depending on 1) the type of mutualistic interaction, and 2) the responsiveness of plant species to mutualistic interactions. In most cases mutualistic interactions increased species performance, therefore, coexistence between pairs of species was observed or predicted by equalizing mechanisms when the inferior competitor obtained larger benefits from the mutualistic interaction than the superior competitor. Veresoglou et al. (2018) show this pattern between obligate and facultative plant interactions with arbuscular mycorrhizal (AM) fungi, and Cardinaux et al. (2018) show it between alpine grasses interacting with soil biota. In contrast, in other cases mutualistic interactions promoted coexistence via niche differentiation as Siefert et al. (2018) show between clover species and soil biota organisms inducing plant nodulation. Interestingly, species were less observed or predicted to coexist when mutualistic interactions, mediated in particular by soil biota, have positive effects in both niche and fitness differences. This is because fitness differences were overall more strongly related to the mutualistic interactions than niche differences, and because the mutualistic interaction tend to benefit all plant species similarly regardless of their competitive ability.

Theoretical and methodological advances to better integrate theory and data.

The main aim of this special feature is to understand plant coexistence through the effects of biotic interactions on the determinants of competitive outcomes (i.e. niche and fitness differences). However, looking at the collection of studies on this special feature, the first challenge that strikes out is the difficulty to integrate theory and data. While some studies have rigorously quantified niche and fitness differences in such way that connect directly with species population dynamics, others have performed experiments in which other competitive metrics have been evaluated and their relationship with niche and fitness differences have been discussed in a qualitative way. We believe that these differences do not diminish the quality of the contributions presented here but rather serve us to highlight the current spectrum of approaches ecologists use to understand plant diversity. Part of the difficulties to integrate theory and data has been that coexistence theory developed by Peter Chesson and colleagues has remained in a highly abstract mathematical language often difficult to translate by empiricists (Barabás et al 2018). In order to bring common bridges of understanding, P. Chesson himself contributes to this special feature with a review paper 1) summarizing the key theoretical concepts by which species can avoid competitive exclusion and therefore coexist, and 2) providing novel concepts to understand the role of biotic interactions in promoting the maintenance of species diversity in multispecies assemblages. Chesson (2018) also provides detailed definitions in both mathematical and non-mathematical ways of concepts that are key to the theory but were not properly explained before. Specifically, he justifies why an average fitness is a species' property, and to which extent this definition differs from the fitness defined at the individual level within evolutionary contexts. Chesson (2018) also explains the need to account for scaling factors when properly defining average species fitness, and finally shows how these scaling factors are accounted for when the aim is investigating the role of multitrophic

interactions in plant coexistence. A scaling factor basically is a transformation that defines how much offspring a species is able to inherently produce relative to its longevity. For instance, a species with a low fitness is the one that produces a lot viable of seeds but they die soon after, while the counterexample of a species with a high fitness can be the one that produces fewer seeds but they are able to survive much longer.

In this collection of studies, we move forward in methodological terms by providing examples on how to evaluate niche and average fitness differences over a wide variety of systems, environmental conditions and organisms. That is the case of Cardinaux et al. (2018) who provide a model for describing species dynamics in biomass terms. They use it for estimating niche and fitness differences for perennial plants, but it is obvious that it can be directly applied to any other terrestrial and aquatic organisms with similar population dynamics. This present a step forward as the mathematical toolboxes developed so far had been specified only for annual plant systems (Godoy and Levine 2014). Several studies in this special feature stress also the necessity to consider the variability of biotic interactions in space, which can contribute to create a mosaic of coexistence across broad scale (Hart et al. 2017, Maron et al. 2018). This conclusion is shared by Petry et al. (2018) thanks to exploring with a sensitivity analyses how the identity of the species coexisting in a community vary due to an hypothetical but realistic scenario of spatial variation in consumer pressure. For future experimental tests of the spatial mosaic of plant coexistence, we believe particular attention should be given to two studies. Previous to this special feature, Lanuza et al. (2018) presented a modification of the annual plant model to estimate in a quantitative way niche and fitness differences as a continuous function of variation in environmental conditions. Now, Bimler et al. (2018) present a similar approach showing how niche and fitness differences, and therefore the species predicted to coexist, vary continuously as a function of soil P, soil water availability and tree canopy cover. Bimler et al. (2018) recognize that their measure of niche overlap and fitness differences behave somewhat differently to the measures defined by Chesson (2000), but have the clear advantage to account for facilitative effects between plant species.

Advances presented in this special feature do not only involve novel toolboxes or experimental approaches, but also the ability to analyze existing databases with readily available methodologies. This is the case of Verosoglou et al. (2018), who used data from the 'BIODEPTH' grassland biodiversity experiment with the methods developed by Carroll et al. (2011) to successfully estimate the effect of plant responsiveness to arbuscular mycorrhizal fungi on the variation in niche and fitness differences between species. Finally, some studies in this special feature make us aware that antagonisms, mutualisms and environmental conditions can influence plant-plant interactions in non-linear ways (Benadi and Pauw 2018, Bimler et al. 2018), but for most systems the shape of the non-linear response is virtually unknown. Benadi and Pauw (2018) solve some of these uncertainties by showing that the number of visitation of pollinator insects to shrubs species as a function of their abundance in the Cape fynbos follows a unimodal response. Certainly, this pattern presents new knowledge that needs to be tested for its generality in many other systems.

Future challenges

This special feature has served to identify several challenges we should overcome to better understand the struggle for coexistence. As evidenced above, better integrating data and theory still remains an unsolved challenge, especially for complex systems that are hard to manipulate experimentally. While documenting the existence of patterns consistent with theoretical expectations is a first step in the right direction, from a predictive point of view there is still a lot of work to do. However, the main challenge identified is how can we empirically consider the plethora of antagonistic and mutualistic interactions occurring simultaneously. Despite we have a set of mathematical toolboxes available to answer this question, gathering the data needed to test experimentally several interactions simultaneously is prohibitive. The strategy used to overcome this complexity so far has been relying on the natural history knowledge of the study system to select the most important interactions to test. For example, systems where leaf herbivores has been observed to occur abundantly, one can target the main herbivore as a potential factor to study (Tamburini et al. 2018). This is the approach Tamburini et al. (2018) used in experimental enclosures manipulating two factors, herbivore pressure and water availability. This has the advantage of having tractable systems where only a few factor needs to be manipulated, but ignores other potential important sources of variation. In fact, even in this simple two factor scenario, the interactions between factors show complex plant responses (Tamburini et al. 2018). Interestingly, this approach can also reveal that interactions hypothesized to be important have little impact on species coexistence, as illustrated by the small role that pathogens play in structuring clover populations (Parker and Gilbert 2018).

As an alternative to hypothesis-driven experiments, data-driven models are becoming more and more powerful to understand large and noisy datasets (Baker et al. 2018). If the aim is to consider multiple interaction types simultaneously, this comes at the cost of designing virtually unfeasible experiments. With the rise of data availability in ecology (Allan et al. 2018), and the options to automatically monitor interactions (Ma et al. 2018), machine learning models seems a promising tool as they can be trained to identify which interactions matter most from the plethora of potential existing interactions. However, both data availability and model development are far from ready to explore this approach. As an illustrative example, there are to our knowledge only two multitrophic networks considering multiple interaction types (Pocock et al 2012, Kéfi et al. 2016) and these effort decoupled the network topology from fitness measures.

One last challenge identified is the difficulty of upscaling from pairwise interactions to more complex relationships that capture higher order interactions (Billick and Case 1994, Levine et al. 2017). Despite complex non-additive 'higher order' interactions are known to occur in nature (Mayfield and Stouffer 2017), most studies so far, including those in this special feature, model in most cases competitive effects as pairwise effects between species and add the multitrophic effect of interactions with other organisms as an additive linear term to competition.

However, it is still unclear whether additive direct effects can capture all the important details about how interactions between species impact community diversity. As we have discussed above, rather than a theoretical challenge, the challenge is now is to obtain enough information to account empirically for higher order interactions and to validate whether they can predict

better species dynamics than model accounting for a much simpler structure of interactions within and between trophic levels.

Conclusions

Overall, the studies presented in this special feature constitutes a solid base empirically exploring how a diverse range of mutualistic and antagonistic interactions act upon the determinants of competitive outcomes. As first conclusion, experimental studies have shown that biotic interactions seem to act more frequently as equalizing mechanisms rather than stabilizing mechanisms. Future studies with a better experimental design might validate this conclusion as stabilizing mechanisms are often more difficult to evidence. Several studies have presented novel efforts to estimate niche and fitness differences for plant species with a wide range of life-span and along continuous environmental gradients. These advances together with a theoretical update on mechanisms of maintenance of species diversity done by Peter Chesson open novel paths for future research. Collectively, these advances will likely serve to pave the road for a better theoretical and empirical understanding on how biotic interactions control biodiversity.

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