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Review
Phenotypic Plasticity and Species Coexistence

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Ecologists are increasingly interested in predicting how intraspecific variation and changing trait values impact species interactions and community composition. For many traits, much of this variation is caused by phenotypic plasticity, and thus the impact of plasticity on species coexistence deserves robust quantification. Partly due to a lack of sound theoretical expectations, empirical studies make contradictory claims regarding plasticity effects on coexistence. Our critical review of this literature, framed in modern coexistence theory, reveals that plasticity affects species interactions in ways that could impact stabilizing niche differences and competitive asymmetries. However, almost no study integrates these measures to quantify the net effect of plasticity on species coexistence. To address this challenge, we outline novel empirical approaches grounded in modern theory.

The Importance of Phenotypic Plasticity for Species Coexistence

Ecologists are increasingly interested in predicting how species' trait values and phenotypic variation impact species interactions, community composition, and ecosystem function [1–3]. Trait-based ecology is identifying the multifarious impacts of trait-mediated direct and indirect interactions between species on community dynamics [4–6]. Meanwhile, ecologists are increasingly emphasizing the importance of variation within species in influencing ecological processes. A recent meta-analysis reveals that approximately one-fourth of the total trait variation within plant communities is due to variation within species [2]. How this intraspecific variation drives ecological dynamics remains an important open question [1,7,8]. In fact, the ecological consequences of genetically based intraspecific variation coupled to rapid evolution in species traits has blossomed into its own subfield of eco-evolutionary dynamics [9–11]. Nonetheless, for a number of traits, a large fraction of the spatial and temporal changes in species' mean trait values, as well as trait variation within species at a single place and time, is likely attributable to phenotypic plasticity. Thus, an important next challenge in trait-based ecology is to understand the role of phenotypic plasticity in mediating species interactions.

Phenotypic plasticity occurs when a genotype expresses different phenotypes in different environments [12], summarized in Box 1. The conditions that select for plasticity as well as how it mediates adaptive evolution have long been the subject of considerable interest [12–16]. In this review, we aim to bring greater attention to the ecological impacts of plasticity caused by competitive interactions, with particular focus on how plasticity mediates species coexistence. We focus on competitive interactions as they dictate many of the most important processes in community and ecosystem ecology [17,18], and are well known to induce phenotypic changes [19,20]. Examples include diet shifts in tadpoles from omnivory to carnivory [21], transformation of locusts from solitary to gregarious forms [22], elongation of aboveground plant shoots [23], and diet and behavioral shifts in many taxa [20,24–27]. Studies examining the impact of plasticity on species coexistence date back many decades, especially in animal behavioral ecology [28,29] and root foraging behavior of plants – reviewed in [30]. Yet, most of this literature

Trends
Phenotypic plasticity due to competing species can promote or hinder coexistence.

Coexistence theory can guide experiments designed to test the effects of plasticity.

Manipulations of plasticity can robustly test how it modulates competitive outcomes.

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focuses on the beneficial impacts of plasticity, for example, diet niche divergence, without robustly considering how plasticity can hinder coexistence. Thus, we argue that the impact of plasticity on the coexistence of competing species, and hence population and community dynamics, remains unclear [31–38].

Consistent with expectations from classic niche theory, many studies argue that plastic responses to competitors promote coexistence by causing competing species to differ more in their traits [19,25,26,29,36,39–41]. Nonetheless, other studies suggest that coexistence is hindered by plasticity when it compounds competitive advantages [27,40,42–44] and still others suggest no impact [45]. Although some of these conclusions are reached by measuring changes in competitive interactions with plasticity, others simply infer competitive implications from the trait changes themselves. Similarly ambiguous predictions for plasticity effects on competition emerge in the invasion biology literature. Whether successful invaders are more plastic than their less successful counterparts or the residents of the communities they invade is unclear, as is the role of plasticity in determining invasion outcomes [12,46–48].

Given that the current state of the literature is characterized by contradictory results, it remains difficult to predict when and how plasticity promotes or hinders coexistence. Moreover, because most studies rely on verbal arguments based loosely on the notion that trait differences imply niche differences – an overly simplified view of coexistence theory [49,50], we argue that the theoretical expectations are lacking as well. To help make progress on this front, we first briefly review modern coexistence theory and discuss how it helps quantify the impact of plasticity on coexistence. We then critically assess current empirical approaches and results in light of this theory. Finally, we propose empirical approaches that will provide greater insight into the impacts of plasticity on coexistence.

Clarifying the Effects of Phenotypic Plasticity on Coexistence

Many of the contradictory expectations and conclusions emerging in the literature connecting phenotypic plasticity to the outcome of competition can be resolved by incorporating recent advances in coexistence theory. This body of work, formalized by Chesson [49], frames species

coexistence as a competitive outcome determined by the relative strength of stabilizing niche differences that favor coexistence, and average fitness differences that determine competitive exclusion (Figure 1, Key Figure and Box 2). Stabilizing niche differences favor coexistence by benefiting species that drop to low density. They arise from species differences that cause the strength of intraspecific competition to exceed that of interspecific competition. They include, for example, species differences in the resources most limiting growth, differences in their

Key Figure

The Balance Between Competitive Exclusion and Coexistence Mediated by Plasticity
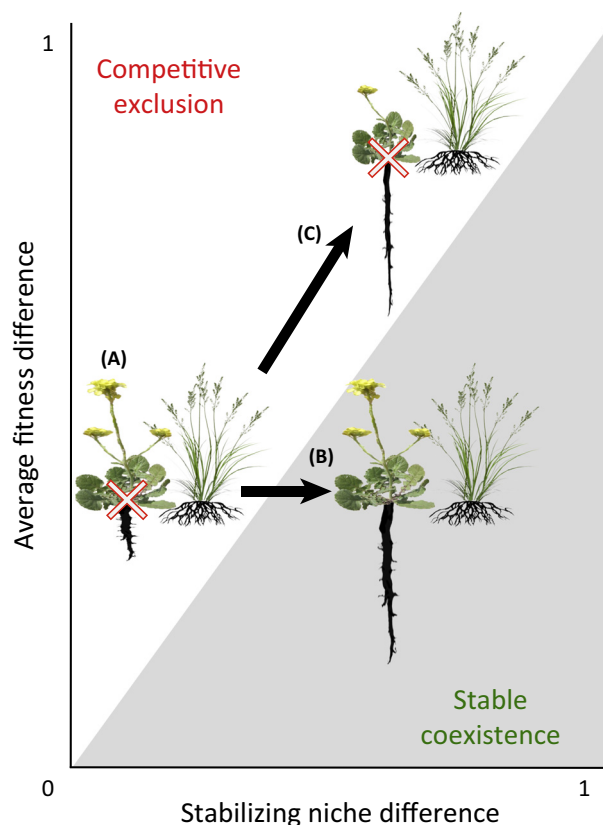
Trends in Ecology & Evolution

Figure 1. Graphical representation of how coexistence is mediated by both the stabilizing niche difference (*x*-axis) and average fitness difference (*y*-axis). Stable coexistence is predicted when the niche difference exceeds the fitness difference (gray area). Otherwise, competitive exclusion is predicted (white area). For example, (A) shows a competing forb and grass, both of which have shallow roots. The grass competitively excludes the forb because the niche difference (indicated by the rooting depth difference) does not compensate for the fitness advantage of the grass (shown by the number of inflorescences). We can superimpose two simple examples of how phenotypic plasticity can affect the outcome of competition, assuming that plasticity causes the forb to develop a deeper tap root. In (B) we see that plasticity increases the niche difference, because the forb now acquires resources deep below the surface, leading to stable coexistence. In (C), however, we see another possible outcome wherein plasticity not only impacts niche differences but also alters fitness differences. Although the forb now accesses deep resources, increasing its niche difference from the grass, the forb loses access to shared limiting resources near the surface decreasing its average fitness, which in this case, leads to its exclusion by the grass. Similar examples could be developed for other systems such as dietary niche divergence in competing fish species (see text).

Box 2. Modern Coexistence Theory Applied to an Annual Plant System.

Stable coexistence reflects the balance between two quantities with opposing effects on the outcome of competition [49]. Stabilizing niche differences favor coexistence by concentrating competition between conspecific individuals to a greater extent than between heterospecific individuals, while average fitness differences drive competitive exclusion by favoring one competitor over others.

Both of these key drivers of competitive outcomes can be identified in mathematical models of competition, as illustrated here for a system of annual plants. The competitive dynamics of two annual species, i and j, can be described as follows:

$$N_{i,t+1} = \frac{\lambda_i N_{i,t}}{1 + \alpha_{ii}N_{i,t} + \alpha_{ij}N_{j,t}} \tag{I}$$

where $N_{i,t}$ is the number of individuals of species i in year t, and λ_i is the per individual seed production in the absence of neighbors. The decline in population growth due to neighbors is described by the term in the denominator, where α_{ij} is the per capita effect of species j on the seed production of species i.

With this model, the stabilizing niche difference is [86]:

$$1 - \sqrt{\frac{\alpha_{ij}\alpha_{ji}}{\alpha_{ii}\alpha_{jj}}} \tag{II}$$

It is a ratio of the strength intraspecific versus interspecific competition coefficients, and determines the degree to which species benefit from dropping to low density.

Meanwhile, the average fitness difference, expressed as a species i's fitness over species j's is

$$\frac{\lambda_i - 1}{\lambda_j - 1} \sqrt{\frac{\alpha_{jj}\alpha_{ji}}{\alpha_{ii}\alpha_{ij}}} \tag{III}$$

The first term is the ratio of species i to j's innate reproductive capacity, while the second term describes the sensitivity of species j to competition from species i and j versus the sensitivity of species i (not the same as the square root term of the niche difference). Competitive superiority for species i results from high innate reproductive capacity, and low sensitivity to competition. This equation determines the frequency-independent competitive advantage of one species over the other, which favors competitive exclusion.

Given that both the niche and fitness differences between competitors can be related to functional traits [52], these quantities can be used to predict how plastic trait responses to neighbors influence the outcome of competition. A more specific point revealed by these equations is that fitness and niche differences share some underlying parameters, and thus functional traits that determine these parameters, and plasticity in these traits, will simultaneously affect both drivers of competitive outcomes.

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interaction with specialist consumers or pathogens, or differences in the spatial environmental locations most favorable for performance [49].

The operation of stabilizing niche differences does not guarantee stable coexistence. Rather the benefits species gain from dropping to low density (and harm they suffer at high density) must be strong enough to overcome their average difference in competitive ability – termed the average fitness difference [49]. Average fitness differences are the frequency-independent advantages and disadvantages that species have relative to one another. Examples include species differences in their ability to deplete a shared limiting resource, differences in reproductive capacity when resources are not limiting, or differences in tolerance of a generalist consumer. In the absence of stabilizing niche differences, fitness differences will drive the exclusion of the species with lower average fitness. This framework can be applied to specific models of interacting competitors (Box 2).

Advances in how we frame questions about species coexistence present several lessons for understanding the effects of phenotypic plasticity on the outcome of competition.

(i) Phenotypic plasticity can promote or hinder coexistence depending on how plasticity affects niche and fitness differences. Predicting whether plasticity benefits or harms coexistence requires understanding its effects on both drivers of competitive outcomes (Figure 2). Various ecological outcomes can therefore arise. Figure 1 (arrow B) illustrates an example wherein plasticity causes a system to move from competitive exclusion to stable
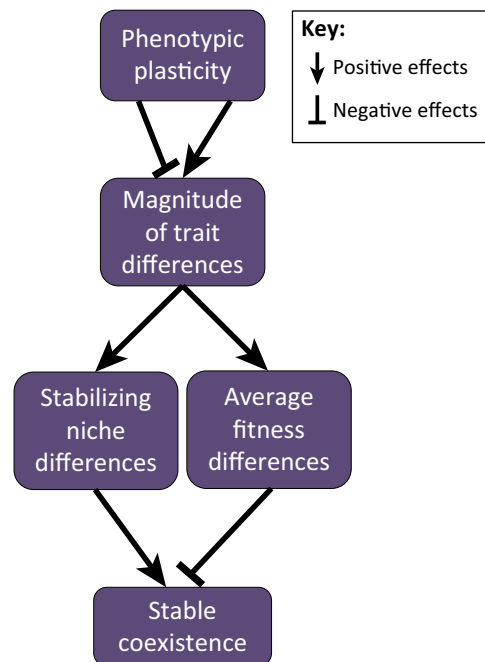
Figure 2. Causal Links Between Plasticity and the Outcome of Competition. Phenotypic plasticity can impact the extent of trait divergence among competing species. Changes in the magnitude of trait differences can then modify both stabilizing niche differences and average fitness differences in various ways. Both of the processes then determine how/ whether plasticity promotes or hinders stable coexistence.

coexistence, as occurs when plasticity enhances the stabilizing niche difference between competitors. Alternatively, if plasticity augments the fitness difference in addition to increasing the niche difference, it might have no benefit for coexistence (Figure 1, arrow C).

Figure 1 involves niche differences that emerge in well-mixed systems, but plasticity could similarly influence the strength of spatial coexistence mechanisms when determining how species differ in their response to spatially heterogeneous environments [35].

(ii) Understanding how plasticity affects both intraspecific and interspecific competition is key to predicting its effects on competitive outcomes. As illustrated in Box 2, the niche differences reflect the degree to which intraspecific interactions are more limiting than interspecific interactions [49]. Thus, the effects of plasticity depend on how it alters the ratio between the strength of intraspecific and interspecific competition. In fact, plasticity that reduces interspecific competition will harm coexistence if the plastic trait change reduces intraspecific competition to an even greater extent. A further lesson is that for plasticity to stabilize coexistence, trait change that occurs when a species drops to low relative abundance must benefit that species over the more common competitor. Thus, the plasticity most relevant to stabilizing niche differences involves the trait change that occurs when moving from a conspecific to a heterospecific competitive environment.

(iii) Knowing how competition alters trait values is insufficient for predicting plasticity effects on competitive outcomes. Recent experiments reveal that trait differences can impact both niche and fitness differences in complex and unexpected ways [51,52]. For instance, results from an 18-species field experiment testing the univariate correlations between functional traits and competitive outcomes found that traits often assumed to reflect niche differences, such as phenology and rooting depth, actually predict fitness differences and not niches differences. Hence, differences in these trait values between species promote competitive

exclusion. In part, this complexity arises because individual traits are related to numerous parameters that contribute to both stabilizing niche differences and fitness differences (Box 2), and plastic changes in one trait are often correlated with changes in others [34].

The State of Empirical Studies in Light of Modern Coexistence Theory

We next critically review current empirical studies of plasticity in light of modern coexistence theory. Although no study fully traces the pathway of causality from trait change to competitive outcomes (Figure 2), each provides valuable insight into how plasticity impacts intermediate steps in the pathway.

Approaches

Testing the impact of plasticity on coexistence is empirically challenging but the number of studies doing so is growing rapidly [31,34]. Experimental manipulations of plasticity in multispecies contexts are very rare [36], so we focus on studies that correlate between-species variation in the extent of their plasticity with measures of interspecific competitive ability or abundance in natural communities. These studies currently assess plasticity in different ways. Some quantify plasticity as the extent of trait change among competition-free individuals growing under different abiotic conditions (e.g., light intensity) [39,44–48,53–55]. Others assess plasticity in competitive settings, but competition *per se* is not manipulated. Trait change is measured in response to varying nutrient levels, community composition, or habitat structural complexity [26,41–43,56–58]. A third approach, and one more relevant to the questions raised here, assesses plasticity by comparing the traits of individuals growing alone versus growing under interspecific competition [19,21,24,25,37,40,56,59–61].

By synthesizing results from studies using one or more of these approaches, we can show how plasticity might affect both the stabilizing niche differences and average fitness differences [31]. Whether these effects ultimately benefit or harm coexistence varies considerably across studies.

Impacts on Stabilizing Niche Differences

Plasticity can shift resource use or resource acquisition traits and sometimes these observations are combined with evidence of reduced interspecific competition [19,26,37,40,61,62]. For example, when subjected to interspecific competition, tadpoles that were phenotypically induced by prior exposure to interspecific competition grew better than those that were not [36]. By contrast, other studies have found that plasticity can lead to trait convergence and increased niche overlap, which should harm coexistence [37,41]. For example, some plant species roots grow preferentially toward heterospecific competitors [63] and such plastic responses could hamper species' ability to coexist on shared soil resources. More complex dynamics, which may include the promotion of coexistence, can result from such root plasticity when species are limited by specialist soil pathogens [63].

Most evidence that plasticity impacts intraspecific interactions comes from empirical and theoretical studies in single-species systems and plants in particular. Nonetheless, because it is the ratio of the strength of intraspecific to interspecific competition that determines stabilizing niche differences, these results can still be relevant for understanding multispecies coexistence. For example, Schiffers *et al.* [64] showed that plasticity in root growth permits plants to minimize rhizosphere overlap and lower intraspecific competition. Because the population is less self-limiting, it should reduce between-species niche differences (Box 2) as long as interspecific competition remains unaffected. By contrast, in both bean and soybean, plasticity in root growth increases the strength of intraspecific competition [65,66], as plants overinvest in roots, which should help stabilize competitive interactions between species. Similarly, a review of 10 studies of fish populations found that higher intraspecific density reduces dietary niche breadth as often as it increases it [67].

Impacts on Average Fitness Differences

Plasticity has also been shown to impact the strength of competitive asymmetries, with likely effects on average fitness differences. Plasticity could help subordinate species minimize their competitive disadvantages. For example, studies of plant competition for light suggest that height plasticity should help alleviate competitive imbalances between species if shorter plants elongate to minimize shading [39,41,58]. Other studies argue instead that such plasticity has no impact on competitive asymmetry [56,68]. For instance, although four *Papaver* species differ greatly in their plastic response to light and nutrient gradients, all species had similar sensitivities to competition from winter wheat and winter rape [45]. Still other studies show that plasticity enables dominant species to increase their competitive impact [40,42–44], which should harm coexistence. For instance, experiments in *Formica* ants reveal that colonies of a dominant species plastically increase the size of their foragers and alter their behavior, when heterospecific competitors are more common, enhancing their competitive advantage [27].

Limitations of Current Approaches

A key lesson from theory is the importance of testing how plasticity impacts both niche and fitness differences when inferring effects on coexistence, something few studies do. For example, several studies suggest that plasticity enables fish to shift their habitat use and prey consumption when in competition, thereby increasing niche differences and promoting coexistence [19,26,29,60]. Yet, if these new prey items are less frequent or less nutritive, this plasticity might give the shifting taxon a frequency-independent disadvantage against its competitor, thus leading to exclusion (see Figure 1 for an example with plant rooting depth).

A second limitation is that the multispecies literature frequently explores the effects of plasticity on interspecific competition, with little simultaneous consideration of the impact of intraspecific competition. This is despite the fact that single-species studies often show strong impacts of plasticity [64,66,67]. The strength of both interspecific and intraspecific competition and species sensitivity to competition can influence the stabilizing niche difference and the fitness difference (Box 2). Of course, studies that simply evaluate trait change in response to competitors are even further removed from the critical information [52].

A third limitation is that plasticity can occur in both members of a species interaction [15] yet many studies draw conclusions from plasticity in only one competitor. Plastic changes in one species promoting coexistence might be countermanded by plastic changes in the other. For example, it is often suggested that short plants can use plasticity to match the height of taller dominant species, favoring coexistence [39,41,58]. Yet, if the dominant species is also plastic it could simply grow taller and maintain its dominance.

Fourth, most of the plasticity measures are not directly relevant to the varying conditions experienced in a competitive dynamic. In particular, the extent of plasticity when growing without any competitors, for example, under abiotic gradients, might not represent the extent of plasticity in response to competition [37,41]. Other studies compare trait values of individuals when growing alone or with heterospecific competitors, but miss their response to conspecific competitors. As noted earlier and following from Box 2, the plasticity most relevant to stabilizing niche differences concerns trait change from conspecific to heterospecific neighborhoods; these are the conditions that change when species drop from common to rare.

A final limitation concerns the constraints arising from failing to experimentally manipulate plasticity itself, an acknowledged empirical challenge [34]. If one is comparing across species that differ in their plasticity, the effects of plasticity might be confounded by a number of other differences

between species [31,34]. If one instead is comparing the same species growing alone or under heterospecific competition, it is difficult if not impossible to assign changes in performance to plasticity because plasticity is confounded by the treatment (presence of competitor) that induces it [31]. In general, attributing ecological success or a perceived reduction of interspecific competition to plasticity can be difficult without a proper control [37,39]. Developing better methods to address this issue forms one of the paths forward in this research area.

Looking Forward

Current empirical results suggest that plasticity induced by competitors can have diverse impacts on both niche and average fitness differences. However, the conclusions reached in these studies are often based on an incomplete assessment of the processes that determine stable coexistence. To properly test the impact of plasticity on coexistence, incorporating the lessons of modern theory, one needs to quantify how plasticity, caused by both intraspecific and interspecific competitors, impacts the strength of both intraspecific and interspecific competition and other parameters determining competitive outcomes, for example, intrinsic growth rates (Box 2). Our review suggests that the most significant progress will come from studies that (i) experimentally manipulate plasticity [31,34], and (ii) explore the impact of this manipulation on competitive dynamics.

Manipulating Plasticity

First, investigators can use one of several approaches to manipulate the potential for a plastic response. These include (i) using genetic engineering to create low and high plasticity taxa from a single identical source; (ii) applying RNA interference methods that silence or constitutively express plastic traits; or (iii) artificially selecting taxa to differ in their extent of plasticity. For an example of the first approach, Schmitt *et al.* [69] used transgenic tobacco and *Brassica rapa* that either never responded to shading or always grew as though shaded to test whether plasticity in stem height, allometrically adjusted by dry biomass, was adaptive. Although all of these methods could have pleiotropic effects on traits other than plasticity, manipulating the potential for a plastic response seems a promising avenue in many systems. We emphasize that because coexistence is a multispecies problem, the next step involves applying these methods in a multispecies context, simultaneously manipulating the plasticity of several competitors.

A second approach to manipulating plasticity involves inducing alternative phenotypes with cues. This approach will only be successful if the plastic response lasts longer than the cues that induce it. Depending on the system, one can mimic the presence of a competitor using light cues, infochemicals (e.g., kairomones), or tactile and visual stimuli to induce the plastic response. The key challenge is ensuring that the cue itself has little impact on the focal organism other than inducing plasticity. For example, Dudley and Schmitt [70] cleverly induced plasticity by modifying the red to far-red light ratio experienced by a plant, which mimics the presence of a competitor [23] without impacting the total amount of photosynthetically active radiation. Similar experiments should be possible with other cues such as root exudates or volatiles.

Alternatively, if the cues used to detect competitors are not well characterized or not easily manipulated, one can use temporary competitors during the early stages of growth to induce plasticity. Once plasticity is induced, the impact of plasticity on competition can be tested separately. For example, in one of the most robust tests of the impact of plasticity on competitive interactions to date, Relyea [36] induced wood frog tadpoles with conspecific or heterospecific competitors. Tadpoles previously induced by heterospecific individuals had higher growth rates when subjected to heterospecific competition. This study exemplifies the value of exploring the consequences of competitive induction by both conspecific and heterospecific competitors (or their cues), and doing so for multiple competitors.

Inferring Impacts on Competitive Outcomes

Studies that manipulate plasticity must next connect the measured competitive responses of individuals to the outcome of competition between species (Figure 2). The best approach for doing so will depend on the study system. In systems in which multigenerational community dynamics occur on short time scales, one can directly observe whether plasticity alters the time to competitive exclusion, the relative abundance of coexisting species, or the outcome of reciprocal invasion experiments [71]. Such experiments might require the use of single clonal populations to eliminate the possibility of evolutionary changes that would confound the impact of plasticity. In other systems, mechanistic or phenomenological models are necessary to predict how plasticity impacts the outcome of competition. Detailed eco-physiological experiments can be used to measure plastic changes in resource acquisition rates and resource requirements [35,72], and relate these to competitive outcomes in mechanistic competition models. Alternatively, phenomenological models of competition can be parameterized with competition coefficients inferred from response surface experiments conducted with individuals induced with various stimuli [52]. These same model parameters can also be measured in observational studies, but it would be challenging to avoid confounding the impact of plasticity with the impact of competition itself. Analysis of the parameterized mechanistic and phenomenological models can be used to reveal how plasticity alters both niche and fitness differences and ultimately coexistence (Box 2).

Future Theoretical Directions

One of the central messages of modern coexistence theory is that frequency-dependent dynamics are key to stable coexistence (Box 2, [49,50]). The challenge when incorporating the effects of plasticity into this body of work is that plasticity can stabilize or destabilize interactions through two fundamentally different pathways. First, as noted throughout our paper, plastic responses can influence coexistence by differentially affecting intraspecific versus interspecific interactions (the stabilizing niche difference). Second, even if plasticity simply favors the competitive ability of one species over another (a frequency-independent fitness advantage), if the induction of that plastic response is itself frequency dependent, its effect might be to stabilize (or destabilize) the interaction. This complexity is worthy of theoretical development. The growing number of models focused on eco-evolutionary feedback as well as more classic character displacement theory [73–75] could be adapted, or even simply reinterpreted, to explore the impacts of the very rapid trait change associated with plasticity [11].

Concluding Remarks

Studying the impact of phenotypic plasticity on coexistence is challenging for both theoretical and methodological reasons. Yet, understanding its impact on community composition and ecosystem function is of the upmost importance because of its ubiquity and potential significance [6,12,15,33,34]. The studies we discussed here have provided valuable insights into how plasticity impacts species interactions. Yet, because of the limitations discussed, we must conclude that we still know relatively little about the effects of plasticity on coexistence (see Outstanding Questions). Better knowledge will continue to accrue with the central place of plasticity in studies of intraspecific variation, trait-mediated interactions, and eco-evolutionary dynamics [6,8–10,76]. Nonetheless, these findings must be complemented by research specifically targeting plasticity effects on coexistence along the lines of the empirical approaches grounded in theory that we have outlined here. Further progress on both the empirical and theoretical front should culminate in a more general integration of plasticity, intraspecific variation, and rapid evolution into community ecology.

Outstanding Questions

Are plastic traits, induced by competition, more likely to impact stabilizing niche differences or fitness differences?

Does the extent of trait plasticity correlate with its importance in dictating species coexistence?

Is plasticity likely to promote species coexistence in spatially or temporally variable environments?

How do plastic and rapid evolutionary changes interact to modulate the outcome of species competition?

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