Reports

Ecology, 0(0), 2021, e03346

How mutualisms influence the coexistence of competing species

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Citation: Johnson, C. A. 2021. How mutualisms influence the coexistence of competing species. Ecology 00 (00):e03346. 10.1002/ecy.3346

Abstract. Mutualisms are ubiquitous in nature and are thought to play important roles in the maintenance of biodiversity. For biodiversity to be maintained, however, species must coexist in the face of competitive exclusion. Chesson's coexistence theory provides a mechanistic framework for evaluating coexistence, yet mutualisms are conspicuously absent from coexistence theory and there are no comparable frameworks for evaluating how mutualisms affect the coexistence of competiting species. To address this conceptual gap, I develop theory predicting how multitrophic mutualisms mediate the coexistence of species competing for mutualistic commodities and other limiting resources using the niche and fitness difference concepts of coexistence theory. I demonstrate that failing to account for mutualisms can lead to erroneous conclusions. For example, species might appear to coexist on resources alone, when the simultaneous incorporation of mutualisms actually drives competitive exclusion, or competitive exclusion might occur under resource competition, when in fact, the incorporation of mutualisms generates coexistence. Existing coexistence theory cannot therefore be applied to mutualisms without explicitly considering the underlying biology of the interactions. By discussing how the metrics derived from coexistence theory can be quantified empirically, I show how this theory can be operationalized to evaluate the coexistence consequences of mutualism in natural communities.

Key words: *coexistence theory; competition; mycorrhizal interactions; pollination mutualisms.*

Introduction

For biodiversity to be maintained, species must be able to coexist with their competitors. From a theoretical perspective, Chesson's coexistence theory (Chesson 2000) is a rigorous mathematical framework for evaluating coexistence mechanisms in consumer–resource interactions involving exploitative competition for resources or apparent competition mediated by shared enemies or both. Yet, the ideas of coexistence theory have not been explicitly applied to the case of mutualism. The conceptual gap is surprising given that mutualisms are ubiquitous in nature and are thought to play critical roles in the maintenance of biodiversity (Bronstein 2015). Unlike other consumer–resource interactions, mutualisms are reciprocally beneficial interactions in which species acquire mutualistic commodities—resources or services that increase the fitness of the recipient species—from their mutualistic partners. The effects of mutualisms on competitor coexistence can therefore be complicated. On one hand, mutualisms increase species' fitness, potentially buffering species from competitive exclusion and favoring competitor coexistence. On the other hand, mutualistic commodities are themselves often limited in nature (e.g., Mitchell et al. 2009), so that species must compete, both intraspecifically and interspecifically, for commodities (Jones et al. 2012). In pollination mutualisms, for example, pollinators compete for floral resources provided by shared plant species and plants compete for the attention of shared pollinator species. What remains unclear is how mutualisms influence competitor coexistence: for example, how do pollinators affect the coexistence of competing plant species?

We lack a coexistence theory framework for mutualism. This is a significant conceptual gap because it leaves the mechanisms of biodiversity maintenance largely unresolved for some of the most common and ecologically important interactions on Earth. Developing a

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Manuscript received 14 October 2020; revised 1 February 2021; accepted 22 February 2021. Corresponding Editor: Bruce E. Kendall.

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coexistence theory framework for mutualism will provide, for the first time, a unified theory of coexistence that applies to three fundamental types of species interactions: competition, consumer–resource, and mutualism. Developing such a framework is challenging, however, because mutualisms entail a biology that is fundamentally different from other consumer–resource interactions. For example, competitors can simultaneously harm each other by depleting mutualistic commodities upon which both species rely *and* indirectly benefit one another via their mutualisms with those shared partners, potentially alleviating competition for the commodities produced by those partners (Johnson and Bronstein 2019). Moreover, mutualisms can also drive positive density dependence that causes competitors' per capita growth rates to decrease as their density declines and increase as their density increases. Mutualisms can therefore predispose species to extinction when they are rare and favor abundant competitors, potentially driving priority effects or even unbounded population growth in models. Indeed, from a mathematical perspective, the potential for infinite population growth means that existing coexistence theory cannot be applied to mutualisms by simply reversing the signs of the interaction coefficients. We therefore require a new coexistence theory framework that explicitly considers the underlying biology of mutualisms.

Mutualisms influence competitor coexistence both by stabilizing (or destabilizing) density-dependent interactions (niche differences in coexistence theory) and by giving one species an average competitive ability advantage over its competitors (fitness differences in coexistence theory). Quantifying niche and fitness difference metrics that explicitly reveal these effects will help to resolve opposing theoretical predictions as well as guide empirical research. For example, some models predict that mutualism can favor competitor coexistence by providing opportunities for niche differentiation (e.g., Pauw 2013). Conversely, other models predict that mutualism can drive competitive exclusion by favoring abundant competitors (e.g., Levin and Anderson 1970). Deriving metrics that bridge these theoretical gaps will allow empiricists to make unified and theoretically justified predictions about how mutualisms affect competitor coexistence.

Here I develop a coexistence theory framework for mutualism by deriving new interaction coefficients to investigate the effects of mutualism on both niche and fitness differences between competitors, using pollination and mycorrhizal mutualisms as illustrative systems. I use these metrics to evaluate how mutualisms affect the coexistence of species (e.g., plants) that compete for mutualistic commodities and (implicitly) for other limiting resources (Fig. 1). I show that failing to account for mutualisms can lead to erroneous conclusions, for example, that species appear to coexist when the inclusion of mutualism drives competitive exclusion, or vice versa.

MATERIAL AND METHODS

To investigate how mutualisms affect competitor coexistence, I develop a model (illustrated in Fig. 1) in which two plant species (at densities N_i and N_j) interact with any number of pollinator species (at density M_k for species k) and compete implicitly (for tractability) for other resources, such as soil nutrients (see Appendix S1). The dynamics of plants and pollinators are given by

$$\frac{dN_i}{dt} = N_i\left(b_i - c_{ii}N_i - c_{ij}N_j\right) + \sum_k e_{ik}M_k\left(\frac{v_{ik}N_i}{1+\sum_j v_{jk}\tau_{jk}N_j/M_k}\right), \tag{1a}$$

$$\frac{dM_k}{dt} = M_k(\beta_k - \delta_k M_k) + \sum_i \frac{\mu_{ik}M_k}{1+\sigma_{ik}M_k}\left(\frac{v_{ik}N_i}{1+\sum_j v_{jk}\tau_{jk}N_j/M_k}\right). \tag{1b}$$

The first term in Eqs. 1a and 1b gives the population growth rates of plants and pollinators, respectively, in the absence of mutualism. Plant species i has a per capita birth rate b_i ($b_i > 0$ when it relies facultatively on pollinators and $b_i = 0$ when it relies obligately on pollinators). The coefficients c_{ii} and c_{ij} quantify intra- and interspecific resource competition, respectively, for species i. Pollinator species k has a per capita birth rate β_k ($\beta_k > 0$ when it relies facultatively on plants and $\beta_k = 0$ when it relies obligately on plants) and suffers density-dependent mortality, δ_k.

The second term in Eqs. 1a and 1b gives the effects of mutualism on plant and pollinator population growth rates, respectively. The function $v_{ik}N_i/(1+\sum_j v_{jk}\tau_{jk}N_j/M_k)$ describes the interactions between plant species i and pollinator species k, where v_{ik} is the visitation rate. In the model, pollinators are either foraging (and thus available to plants) or are currently engaged with a plant (and thus temporarily unavailable to other plants), as defined by an interaction time, τ_{ik}, analogous to a handling time in consumer–resource models. Pollination benefits saturate as plant densities increase relative to pollinator densities (N_j/M_k) as pollinators spend more time engaging with plants and less time foraging. Thus, plants compete for services in the model by attracting pollinators and thereby depriving competitors of access to those services. Plant species i obtains service commodities of value e_{ik} from pollinator species k and confers resource commodities of value μ_{ik}. To prevent unbounded population growth in the model, pollinators acquire resource commodities from plants at saturating rates, as defined by a saturation constant, σ_{ik}.

The model makes some simplifying assumptions for tractability. Resources and commodities contribute additively to plant population growth; thus, a plant species is

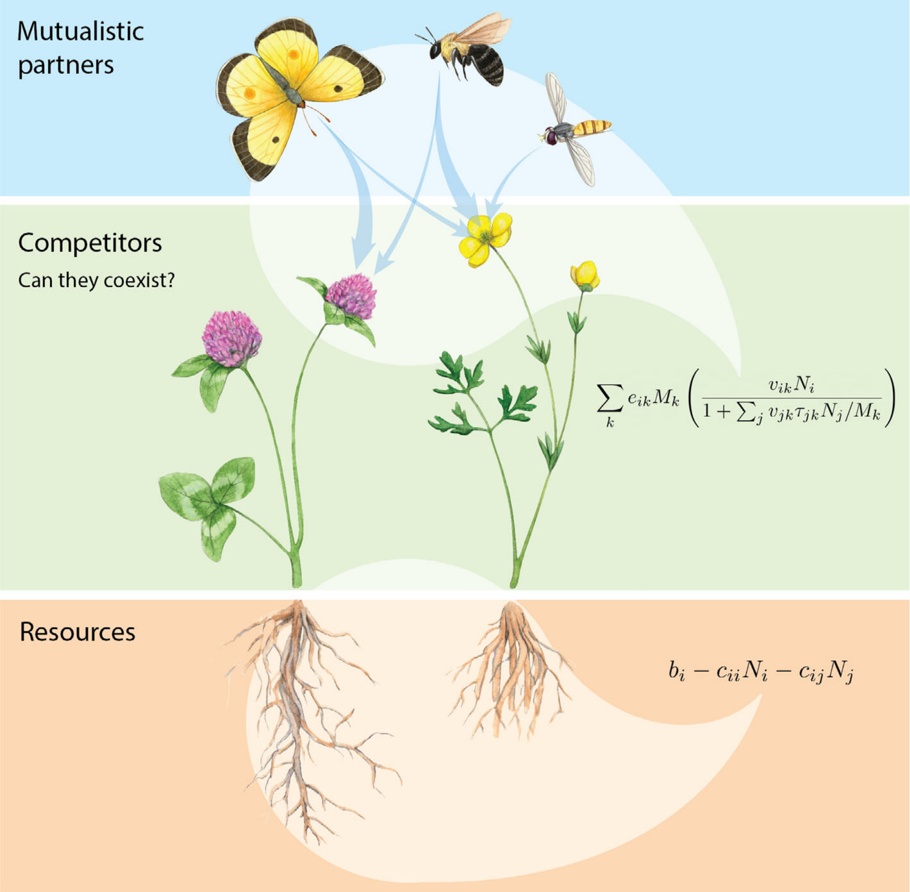

FIG. 1. Conceptual illustration of the framework for resource-for-service mutualisms, exemplified by plant–pollinator interactions. The model evaluates whether two plant species (competitors; middle green region) can coexist when they interact with pollinators (mutualistic partners; top blue region) and compete for other factors such as soil nutrients (resources; lower brown region). Blue arrows illustrate plant–pollinator interactions with the thickness of the arrow indicating the visitation rate. Bubbles highlight the mutualistic and competitive interactions that are described by the associated mathematical functions (see Eq. 1). Resource-exchange mutualisms, exemplified by plant-mycorrhizal interactions, are considered in Appendix S2. Illustrations by Julie Johnson (Life Science Studios).

obligate when it cannot persist on resources alone (i.e., $b_i = 0$) and is facultative otherwise. Plant-produced commodities (e.g., nectar) are also not explicitly incorporated into the model, and there are no explicit costs of producing these commodities. In principle, such costs could be included via additional density-dependent terms in Eq. 1a, which would contribute to plant self-limitation, c_{ii}. Interspecific competition among pollinators is assumed to be weak relative to density-dependent mortality, δ_k, arising due to other factors (e.g., competition for nesting sites). Lastly, interference competition due to the deposition of heterospecific pollen is not explicitly modeled; however, its effects could be considered by increasing τ_{jk} in Eq. 1a to reflect lower pollen transfer efficiency.

Importantly, other mutualisms involve the exchange of resource commodities, exemplified by plant–mycorrhizal mutualisms. I model mycorrhizal mutualisms in Appendix S2 by incorporating commodities produced by mycorrhizae (at rate θ_k, supply constant S_k) as depletable quantities for which plants must compete. All results reported here can be readily applied to resource-exchange mutualisms, such as plant–mycorrhizae, simply by setting $S_k = 1$ and $\theta_k = 1/\tau_{jk}$ in Appendix S2.

Effects of mutualism on density-dependent interactions within and between plant species

My goal is to derive metrics that reveal how mutualisms affect plant coexistence via the niche and fitness difference concepts from coexistence theory. A challenge is that niche and fitness differences are classically derived from the Lotka-Volterra competition model (Chesson 2000), which does not include mutualistic interactions. I therefore follow ideas from MacArthur's derivation of the Lotka-Volterra competition model from a more mechanistic consumer–resource model by using time-scale separation between consumers and their resources to derive explicit formulas for the Lotka-Volterra competition coefficients (MacArthur 1970, Chesson 1990).

I apply timescale separation under the assumption that pollinators often have much shorter generation times than do plants, such that pollinators attain their equilibria ($\mathrm{d}M_k/\mathrm{d}t = 0$) on the timescale of plant population dynamics. Using timescale separation, the density-dependent effects of plant species j on plant species i, α_{ij}, and the per capita population growth rate, r_i, are

$$\alpha_{ij} = \frac{1}{r_i}\left(\overbrace{c_{ij}}^{\text{Resource competition}} + \overbrace{\sum_k e_{ik} v_{ik} v_{jk} \tau_{jk}}^{\text{Competition for commodities}} - \overbrace{\sum_k \frac{e_{ik} v_{ik} v_{jk} \mu_{jk}}{\delta_k}}^{\text{Indirect effects mediated by mutualistic partners}}\right), \tag{2a}$$

where

$$r_i = \overbrace{b_i}^{\text{Per capita population growth rate on resources}} + \overbrace{\sum_k \frac{e_{ik} v_{ik} \beta_k}{\delta_k}}^{\text{Per capita population growth rate on commodities}} \tag{2b}$$

(see Appendix S1 for derivation). Eq. 2a shows that the density-dependent effects encapsulated within α_{ij} are driven by three key biological processes: resource competition, competition for mutualistic commodities, and the indirect effects of plants on each other mediated by their shared pollinators, all relative to the per capita growth rate, r_i. Plant species j harms plant species i via competition for both resources and commodities (the first two terms of Eq. 2a). The strength of competition for commodities is determined by how effectively plant species i attracts pollinators and the value of their services ($e_{ik}v_{ik}$) relative to how effectively plant competitor j attracts and retains these shared pollinators ($v_{jk}\tau_{jk}$). Unlike in classical coexistence theory, plants can also indirectly benefit each other via their mutualisms with shared partners, weakening the per capita competitive effect of species j on species i (the third term of Eq. 2a). For example, plant species j indirectly benefits species i by buoying the fitness of the pollinators upon which species i relies.

There is net facilitation ($\alpha_{ij} < 0$) when the indirect benefits of plant j on plant i mediated by shared partners overcome its competitive effect for both resources and commodities. I constrain $\alpha_{ii} > 0$ and $\alpha_{jj} > 0$ to avoid unbounded population growth, and $\alpha_{ij} > 0$ and $\alpha_{ji} > 0$ because otherwise coexistence simply requires that the species being facilitated limits itself more than its competitor (i.e., $\alpha_{ii} > \alpha_{ji}$ when $\alpha_{ij} < 0$), whereas coexistence is assured when both species facilitate each other.

Eq. 2b shows that the per capita population growth rate, r_i, depends on species' abilities to acquire resources and commodities in the absence of any competition. In this model, r_i must be positive or species exhibit unbounded population growth. The model can nonetheless be applied to both facultative and obligate plants, except in the extreme case when a plant species and *all* of its partners are obligate ($r_i = 0$). In this case, additional sources of negative density dependence not included in this model are required for stability (Johnson and Amarasekare 2013).

Incorporating mutualisms into the coexistence theory framework

In the coexistence theory framework (Chesson 2000), interaction outcomes depend upon niche differences that stabilize competition by causing each species to limit themselves more than their competitors and fitness differences in their overall competitive ability. Coexistence requires that

$$\rho < \frac{\kappa_2}{\kappa_1} < \frac{1}{\rho}, \tag{3}$$

where ρ is the niche overlap and κ_2/κ_1 is the fitness difference. Niche overlap is given by

$$\rho = \sqrt{\frac{\alpha_{12}\alpha_{21}}{\alpha_{22}\alpha_{11}}} \tag{4}$$

and the stabilizing niche difference is $1 - \rho$. Mutualisms can stabilize or destabilize coexistence by increasing or decreasing niche overlap, respectively. The fitness difference, κ_2/κ_1, is given by

$$\frac{\kappa_2}{\kappa_1} = \sqrt{\frac{\alpha_{12}\alpha_{11}}{\alpha_{21}\alpha_{22}}}. \tag{5}$$

In this model, fitness differences reflect how plants are, on average, harmed by competition (for both resources and commodities) and favored by mutualism. Mutualisms can accentuate fitness differences by favoring superior competitors or equalize them by favoring inferior competitors.

Substituting the α_{ij} coefficients from Eq. 2a into these equations (Appendix S1) allows the parameters from the underlying mutualism model (Eq. 1) to determine the niche (Eq. 4) and fitness (Eq. 5) differences. All analyses were performed in Mathematica (v. 12.0).

RESULTS

To illustrate why mutualisms matter for coexistence, I will investigate four scenarios as case studies that show that failing to account for mutualism can lead to erroneous conclusions about plant coexistence. The first scenario demonstrates that mutualisms affect coexistence even when commodities are not limiting. The second scenario highlights that mutualisms can promote plant coexistence even when they do not stabilize plant competition. The third scenario illustrates that mutualisms can drive competitive exclusion when plant species would otherwise coexist. In these scenarios, I have parameterized the model as depicted in Fig. 1, with pollinator 1 preferentially visiting plant 1, pollinator 2 preferentially visiting plant 2, and pollinator 3 exclusively visiting plant 2. The fourth scenario (without pollinator 3 for clarity) evaluates how systematic changes in parameters within the interaction coefficients (Eq. 2) simultaneously modify the niche and fitness differences (See Appendix S3: Table S1 and Appendix S4: Table S1 for parameter values).

Scenario 1: Mutualisms influence plant coexistence even when commodities are not limiting

A key prediction of this framework is that mutualisms can affect plant coexistence even when plants are not limited by commodities, and therefore do not compete for commodities. This is because indirect interactions between the plant species mediated by their mutualistic partners can differentially alleviate the effects of interspecific versus intraspecific resource limitation. To illustrate how these indirect interactions affect plant coexistence, I have parameterized the model such that niche overlap on resources alone is insufficient to overcome a large fitness difference favoring plant 1. Thus, plant 2 is competitively excluded on resources alone (as indicated by the location of green diamond associated with S1 in Fig. 2a). I consider two cases.

In the first case, both plant species are more rewarding to the mutualistic partners upon which they differentially rely (i.e., $\mu_{11} > \mu_{12}$ and $\mu_{22} > \mu_{21}$ in Appendix S3: Table S1), which causes intraspecific resource competition to be weakened relative to interspecific resource competition for both plant species and drives a priority effect (as indicated by the location of the black circle associated with S1a in Fig. 2a). Priority effects have only recently been framed within the context of coexistence theory (Ke and Letten 2018) and this case illustrates how mutualisms can drive priority effects. If one of the plant species—even the inferior resource competitor—is sufficiently abundant initially and differentially rewards its own partners, it can effectively cultivate a partner community that favors itself, thereby allowing it to exclude its competitor competitively.

In the second case, partner 2, upon which the inferior resource competitor (plant 2) primarily relies, obtains greater mutualistic benefits from the plant species than does partner 1, upon which the superior resource competitor (plant 1) primarily relies ($\mu_{12} > \mu_{11}$ and $\mu_{22} > \mu_{21}$ in Appendix S3: Table S1). In this case, the mutualisms

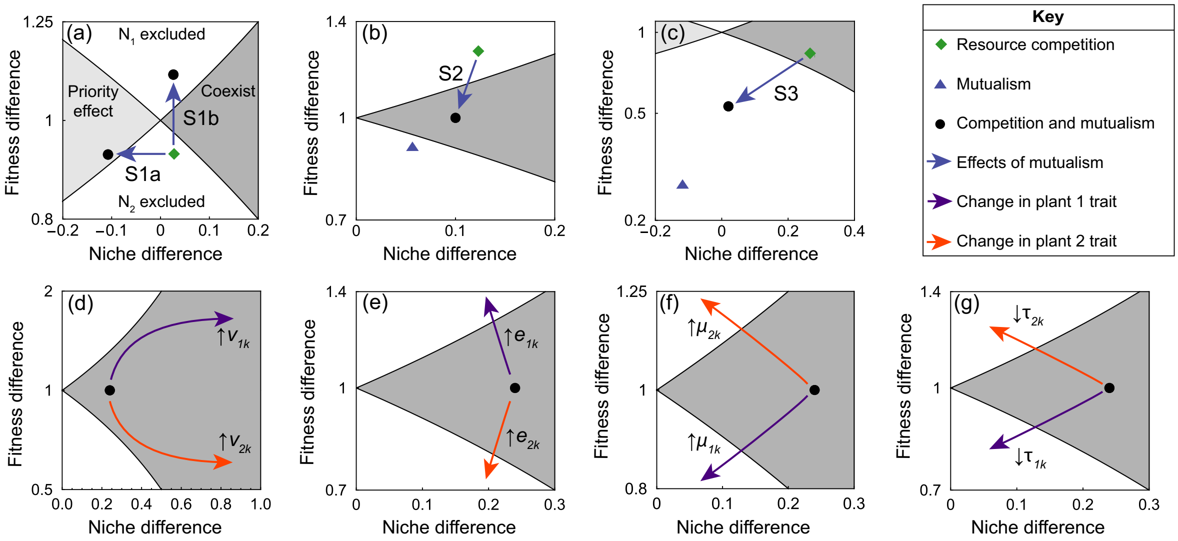

FIG. 2. Mutualism and competition influence plant coexistence by modifying both the niche difference ($1 - \rho$) and the fitness difference (κ_2/κ_1). Interaction outcomes are labeled in panel (a). Plants coexist in the dark gray region when the niche difference overcomes the fitness difference; that is, $\rho < \kappa_2/\kappa_1 < 1/\rho$. Competitive exclusion occurs in the white regions and a priority effect occurs in the light gray region. Points give interaction outcomes predicted by niche and fitness differences due to resource competition alone (green diamond), the effects of mutualism alone (blue triangle; with $c_{ij} = c_{jj}$ for both plant species), and both competition and mutualism (black circle). Blue arrows indicate how the niche and fitness differences change as a result of the mutualisms. Panels (a–c) are for scenarios 1, 2, and 3, respectively. Panels (d–g) are for scenario 4 and illustrate how the niche and fitness differences change as v_{ik}, e_{ik}, μ_{ik}, and τ_{ik}, respectively, are systematically varied for each plant species i. See Appendix S3: Table S1 for parameter values and Appendix S4: Table S1 for the values of the niche and fitness differences for each scenario.

actually reverse the outcome of resource competition (as indicated by the location of the black circle associated with S1b in Fig. 2b). Given this model parameterization, the niche difference remains largely unchanged because the mutualisms reduce inter- and intraspecific resource limitation on the inferior resource competitor, α_{21}/α_{22}, roughly equally. By differentially alleviating the effects of resource competition on the inferior resource competitor (i.e., by reducing $\alpha_{21}\alpha_{22}$ relative to $\alpha_{12}\alpha_{11}$), however, the mutualisms cause the fitness difference favoring plant 1 to be reversed to favor plant 2. That is, by differentially benefiting from the mutualisms, plant 2 actually limits itself less strongly on resources than it limits plant 1 ($\alpha_{12} > \alpha_{22}$). In sum, scenario 1 shows that mutualisms alter competitive outcomes by mediating indirect plant-–plant interactions, even in the extreme case when commodities are not limiting.

Scenario 2: Mutualisms can promote coexistence even when they do not stabilize competition

Mutualisms are often thought to promote plant coexistence by providing opportunities for niche partitioning (Pauw 2013), thus reducing the niche difference. Niche partitioning, however, is not the only mechanism promoting coexistence. Mutualisms can even favor coexistence when they do not stabilize competition. I have parameterized the model so that the niche difference is equal on resources and commodities alone, but the fitness difference on resources favors plant 2, the superior resource competitor. Therefore, independent of the mutualisms, plant 1 is competitively excluded on resource alone (green diamond in Fig. 2b). The fitness difference on commodities, however, favors plant 1, the superior competitor for commodities. Thus, given neutral resource competition, plant 2 is excluded via competition for commodities (blue triangle in Fig. 2b). (Note that, as intraspecific resource limitation is required to prevent unbounded population growth, the outcome of competition for commodities alone is assessed by setting $c_{ij} = c_{ji} = c_{ii} = c_{jj}$ in Eq. 2).

When resource competition and mutualism are considered together, the plants are revealed to coexist (black circle in Fig. 2b). The mutualisms, however, do not promote plant coexistence by stabilizing competition through increasing the niche difference. In fact, the mutualisms slightly destabilize competition in this scenario by increasing the strength of interspecific to intraspecific limitation, reducing the niche difference. Rather, mutualisms promote plant coexistence in this scenario by reducing the fitness difference and thus equalizing competition. This equalizing effect occurs because plant 1 is the superior resource competitor, but is also more sensitive to competition for commodities, whereas plant 2 is the superior competitor for commodities, but is also more sensitive to resource competition. The important point here is that mutualisms can also promote coexistence by reducing the fitness differences favoring superior resource competitors.

Scenario 3: Mutualisms drive competitive exclusion when plants would otherwise coexist

Mutualisms can even drive competitive exclusion when the species would otherwise coexist. To illustrate this point, I have parameterized the model so that niche differences on resources alone overcome the resource-based average fitness difference favoring plant 1, the superior resource competitor. Therefore, the plant species coexist independent of the mutualisms (green diamond in Fig. 2 c). Niche differences on commodities alone, however, are insufficient to overcome the large commodity-based fitness advantage of plant 1, the superior competitor for commodities. Thus, plant 1 excludes plant 2 via competition for commodities alone (blue triangle in Fig. 2c).

When the effects of resource competition and mutualism are considered together, plant 1 is revealed to exclude plant 2 (black circle in Fig. 2c) through the joint advantage it gains through resource and commodity competition. In this case, mutualism drives competitive exclusion via two mechanisms. First, the mutualisms increase niche differences as the plant species overlap more in their mutualistic partners than they do in their resources, increasing the overall strength of interspecific to intraspecific competition. Second, because plant 1 is the superior competitor for resources *and* commodities, the mutualisms amplify its average competitive (fitness) advantage. More generally, this scenario highlights that mutualisms do not inherently favor coexistence.

Scenario 4: Systematic changes in the parameters underlying the niche and fitness differences

The previous scenarios were parameterized specifically to illustrate when failing to account for mutualism leads to erroneous conclusions about plant coexistence. In the final scenario, I have parameterized the model so that the plant species are equivalent competitors for resources and commodities ($\kappa_2/\kappa_1 = 1$) and niche differences on resources and commodities are sufficient for coexistence (black circles in Fig. 2d–g). I then systematically varied the following parameters in Eq. 1 while holding all other parameters constant: visitation rate, v_{ik}, the value of pollinator-provided services, e_{ik}, plant-provided benefits to partners, μ_{ik}, and interaction time, τ_{ik}.

Biasing the visitation rate of pollinators towards one of the plant species (i.e., v_{1k} $(1 + x)$ and v_{2k} $(1 - x)$ where x is an incremental change) increased niche and fitness differences nonlinearly (Fig. 2d) by increasing self-limitation of the plant species being preferentially visited (Appendix S5: Fig. S1a). Increasing the value of pollinator-provided services to one species (i.e., e_{ik} $(1 + x)$) slightly reduced the niche difference and increased the fitness difference (Fig. 2e) by increasing the focal plant species' sensitivity to the effects of competition for commodities by conspecifics and heterospecifics (Appendix S5: Fig. S1b). Increasing the value of commodities provided by one plant species (i.e., μ_{ik}

$(1 + x)$) or decreasing its interaction time (i.e., τ_{ik} $(1 - x)$) reduced the niche difference and increase fitness differences (Fig. 2f, g) by decreasing the focal plant species' sensitivity to competition for commodities by conspecifics and heterospecifics (Appendix S5: Fig. S1c, d). These results highlight that mutualisms can have complex effects on coexistence, but that these effects can be disentangled via their influence on the niche and fitness differences.

Discussion

Given that mutualistic commodities can represent limiting factors for which species compete (Jones et al. 2012), mutualisms should influence competitor coexistence. Chesson's coexistence theory (Chesson 2000) provides a rigorous framework for evaluating coexistence in consumer–resource interactions, but until now, it has not explicitly considered the effects of mutualism. Although it is tempting to include mutualisms within existing coexistence theory, predicting how mutualisms affect coexistence requires a novel coexistence theory framework as mutualisms entail a fundamentally different biology. For example, unlike consumer–resource interactions in which competitors only deplete resources (or are only suppressed by their consumers), competing mutualists affect coexistence both by depleting commodities and indirectly via their mutualisms with shared partners (see Johnson and Bronstein 2019). Herein lies the value of the coexistence theory framework derived here, which explicitly considers the biology of mutualisms and reveals how mutualisms affect coexistence via the niche and fitness difference concepts of coexistence theory. The central message is that to understand diversity maintenance, the effects of mutualism on coexistence must be considered alongside those of resource competition and predation.

Recent theory has highlighted the interdependence of the niche and fitness difference metrics of modern coexistence theory (Barabas et al. 2018, Song et al. 2019). In fact, varying parameters in the underlying mutualism model (Eq. 1) will typically modify the niche and fitness differences simultaneously, as especially highlighted in Fig. 2d–g. As such, mutualisms will almost always have complex effects on both the niche and fitness differences underlying interaction outcomes. For example, if the prevailing effect of mutualism was to alleviate plant self-limitation, the niche difference would decline due to increasing inter- to intraspecific competition and simultaneously the fitness difference would shift towards whichever species was least sensitive to competition for commodities (analogous to Fig. 2e–g). Investigating how mutualisms simultaneously modify niche and fitness differences is critical to understanding the effects of mutualism on coexistence. More generally, the effects of mutualisms may be best interpreted via their aggregated effects on coexistence, rather than simply as stabilizing or equalizing mechanisms (see Song et al. 2019).

Future studies can leverage this theory to study several key issues. I will briefly highlight five future directions. First, a potential limitation of modern coexistence theory is that it is founded upon invasion analysis (Barabas et al. 2018). Mutualisms pose a challenge for coexistence theory because they can involve Allee effects that predispose species to extinction when rare, such that species may be unable to invade, but still coexist. Understanding how Allee effects influence coexistence is an important avenue for future theory. Second, mutualistic communities are often very diverse such that mutualisms could enable community coexistence even when species pairs cannot coexist; for example, via intransitive loops in competitive ability. Linking this theory with the structural approach to coexistence (Saavedra et al. 2017) is an intriguing future direction. The models developed here can also incorporate any number of mutualistic partners, allowing one to explore the effects of more-specialized to more-generalized mutualisms on coexistence. Third, theory emphasizes the importance of multiple interaction types for coexistence (e.g., Sauve et al. 2016). The theory developed here unites resource competition, mutualism, and antagonism into coexistence theory, allowing one to consider all three interaction types jointly. Fourth, theory predicts that adaptive foraging by mutualists can strongly influence community dynamics (e.g., Valdovinos et al. 2013). What remains unclear is how adaptive foraging by mutualists mediates coexistence via the niche and fitness differences. Finally, many mutualisms involve cheating, in which species exploit partner-provided commodities, but reciprocate little or not at all. Cheating may affect coexistence within mutualistic guilds by advantaging cheaters—or disadvantaging the species being exploited—in competition with other guild members. The theory presented here can be adapted to model cheating, allowing one to study the effects of cheating—or variation in mutualist quality more broadly (Heath and Stinchcombe 2014)—on diversity outcomes.

From an empirical perspective, how mutualisms affect coexistence and biodiversity remains an open question (Jones et al. 2012, Bronstein 2015). The scenarios in Fig. 2 highlight that quantifying the contributions of mutualism to both niche and fitness differences is essential for predicting coexistence. This framework allows empiricists to predict the effects of mutualism on competitor coexistence in a fairly straightforward manner conducive to both observational and experimental studies. In principle, all that is required are measures of competitors' per capita growth rates (e.g., seed set) as functions of the density of each competitor including conspecifics. These data would allow one to estimate both the r_i (y-intercept) and α_{ij} (slope) terms of Eq. 2 statistically and to predict interaction outcomes (via Eq. 3) in terms of the niche and fitness difference (via Eqs. 4 and 5, respectively). More generally, this framework allows ecologists to make theoretically justified predictions about how mutualisms affect diversity outcomes relevant to the ecological controls of biodiversity, the conservation of native species, or the impacts of invasive species. Therefore, a major implication of this theory is that it allows empiricists to frame and evaluate predictions about how mutualisms affect diversity maintenance rigorously.

ACKNOWLEDGMENTS

I thank Julie Johnson (Life Science Studios) for the beautiful illustrations. I also thank Jonathan Levine, members of the Levine laboratory, and two anonymous reviewers for helpful comments.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3346/suppinfo

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Code (Johnson 2021) is available on Zenodo. https://doi.org/10.5281/zenodo.4595043