

Using niche breadth theory to explain generalization in mutualisms

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Abstract. For a mutualism to remain evolutionarily stable, theory predicts that mutualists should limit their associations to high-quality partners. However, most mutualists either simultaneously or sequentially associate with multiple partners that confer the same type of reward. By viewing mutualisms through the lens of niche breadth evolution, we outline how the environment shapes partner availability and relative quality, and ultimately a focal mutualist's partner breadth. We argue that mutualists that associate with multiple partners may have a selective advantage compared to specialists for many reasons, including sampling, complementarity, and portfolio effects, as well as the possibility that broad partner breadth increases breadth along other niche axes. Furthermore, selection for narrow partner breadth is unlikely to be strong when the environment erodes variation in partner quality, reduces the costs of interacting with low-quality partners, spatially structures partner communities, or decreases the strength of mutualism. Thus, we should not be surprised that most mutualists have broad partner breadth, even if it allows for ineffective partners to persist.

Key words: *cheaters; generalization; mutualism; niche breadth; specialization; symbiosis.*

REFRAMING MUTUALISMS IN TERMS OF NICHE BREADTH

An organism's niche is comprised of multiple climatic, resource, and biotic axes (Hutchinson 1957, reviewed in Holt 2009), and substantial research effort has explored the range of abiotic conditions organisms experience or tolerate and the factors shaping biotic specialization (e.g., Howe 1984, Futuyma and Moreno 1988, Thompson 1994, Waser et al. 1996; Thompson 2005, Thrall et al. 2007, Poisot et al. 2011, Forister et al. 2012, Sexton et al. 2017). Past work has improved our understanding of the evolution of specialization in mutualisms (e.g., Thompson 1994, 2005), but many gaps remain, particularly when it comes to explaining the observed level of variation in partner breadth (i.e., the number or diversity of partners with which a focal mutualist associates) and the factors that may favor mutualists with diverse partners. This is the niche we seek to fill with this article.

There is a widespread expectation that mutualisms are undermined by "cheating," or taking benefits from a mutualist without (fully) reciprocating (Ghoul et al. 2014, Jones et al. 2015). The anticipated, though seldom demonstrated (Frederickson 2017), cheating in mutualisms has led to the prediction that selection should favor ever more specialized interactions (Frank 1996, Thompson 2005, Thrall et al. 2007, Poisot et al. 2011), as mutualists limit their associations to or preferentially reward only highly cooperative partners (Bull and Rice 1991, reviewed in Frederickson 2013). Although

some textbook examples of mutualism were previously considered highly specialized, such as fig–fig-wasp interactions (Janzen 1979), more recent evidence suggests that they are often "many-to-many" rather than "one-to-one" interactions (Machado et al. 2005, reviewed by Hembry and Althoff 2016). Instead, many mutualists simultaneously interact with multiple partners at a given site (Waser et al. 1996, Schluter and Foster 2012, Afkhami et al. 2014a), or across a geographic range (Silverstein et al. 2012, Trøjelsgaard et al. 2015), or serially associate with different partners across their ontogeny (Palmer et al. 2010) rather than specializing on a single "best" partner. Network analyses of defensive, seed dispersal, and pollination mutualisms also highlight that mutualists commonly interact with multiple partners (Fig. 1); in fact, the finding that mutualistic networks are commonly nested (Bascompte et al. 2003, Bascompte 2009) reflects the absence of reciprocally specialized interactions in mutualisms. The rarity of highly specialized mutualisms in nature raises the question: if mutualists should be under selection to limit their associations to one or a few high-quality partners, why are they commonly associated with diverse partners?

Although the literature on cheating in mutualisms has emphasized the evolution of mechanisms that restrict associations or rewards to one or a few high-quality partners (e.g., partner choice and sanctions; Kiers et al. 2003, Heath and Tiffin 2009), we argue that widespread generalization in mutualisms can be more fully understood from the perspective of niche breadth. Under our framework, mutualists that associate with only one or a few partner species or genotypes are specialists and have narrow partner breadth, while mutualists that associate with many partners are generalists and

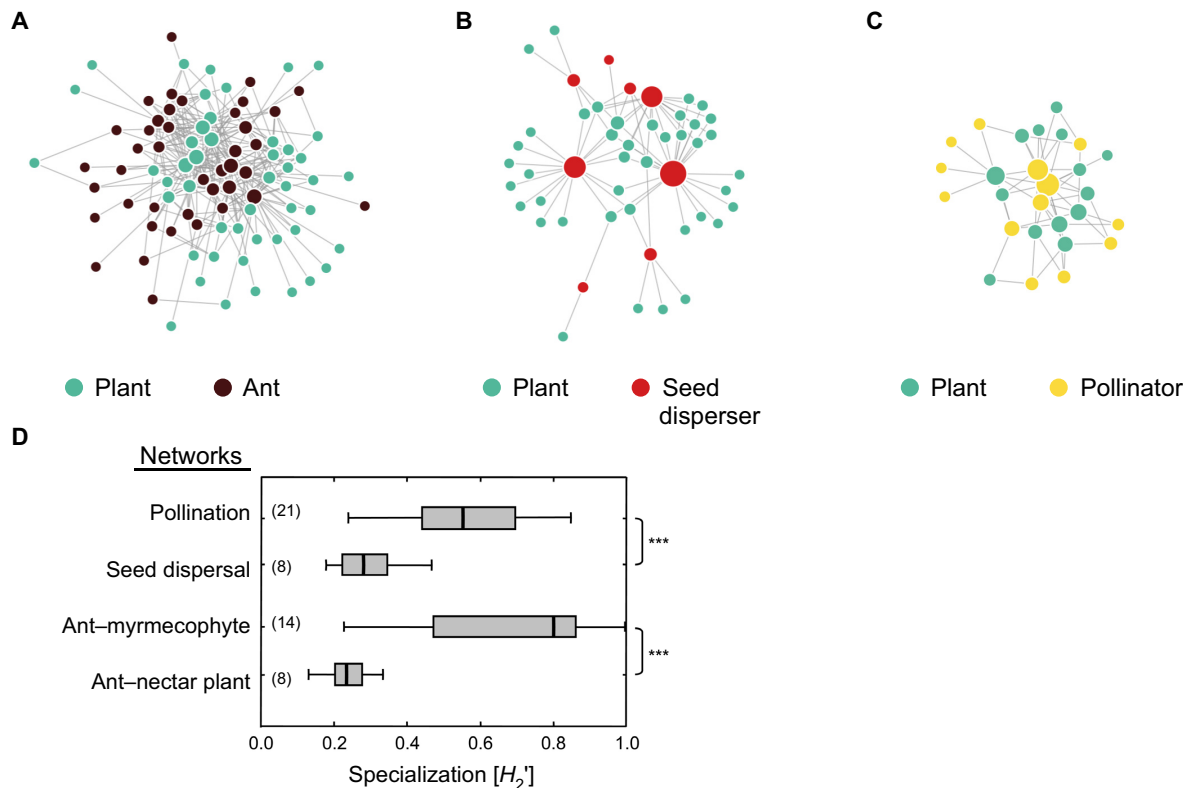


FIG. 1. Mutualistic networks show broad partner breadth is common across systems. Three example networks from the Web of Life (www.web-of-life.es) show focal mutualists associated with multiple partners: (A) plant–ant (Blüthgen et al. 2004), (B) plant–seed-disperser (Heleno et al. 2013), and (C) plant–pollinator (Olesen et al. 2002) systems. (D) Although there is variation across studies and systems in how specialized mutualisms are, many are highly generalized, whereas extreme specialization ($H_2' = 1$) is very rare. Reprinted from Blüthgen et al. (2007) with permission from Elsevier. Numbers in parentheses indicate number of networks. Asterisks show significant differences between network types.

have broad partner breadth. We refer to a focal mutualist and its partners and describe a focal mutualist's partner breadth as its number of associated, functionally similar partner species or genotypes conveying the same type of reward (e.g., different ant defenders of *Acacia* plants), rather than considering multiple partners conferring different rewards (e.g., plants that associate simultaneously with pollinators and ant defenders; for review, see Afkhami et al. 2014a).

Here, we explore how environmental variation in partner availability (i.e., the local partner pool) and partner quality (i.e., the relative fitness benefit a partner confers to a focal mutualist) may selectively favor mutualists having broad partner breadth. Building on foundational work such as Thompson's (2005) geographic mosaic theory of coevolution, our framework places mutualisms in a niche breadth context that allows us to integrate concepts from other realms of community ecology to further explore how multiple partners may benefit a focal mutualist. Additionally, our framework differs from those previously proposed (e.g., Thrall et al. 2007, Poisot et al. 2011) because it does not rely on the assumption that low-quality partners are necessarily cheaters.

Borrowing the concepts of complementarity and sampling effects from the biodiversity–ecosystem function literature (e.g., Loreau and de Mazancourt 2013), we describe how a mutualist may benefit from diverse partners that offer similar rewards through complementary mechanisms or

pathways (e.g., Stachowicz and Whitlatch 2005) and how associating with multiple partners increases the probability of a focal mutualist sampling the best one (e.g., Albrecht et al. 2012). Mutualists associating with diverse partners may also have broad niche breadth along other axes, and we explore how broad partner breadth may be selected for if it expands the range of an organism's abiotic tolerances. In addition, we highlight factors that likely preclude selection for narrow partner breadth, including spatially structured partner populations (e.g., Akçay 2017), a lack of variation in partner quality (e.g., Simonsen and Stinchcombe 2014), reduced cost of low-quality partners (e.g., Argüello et al. 2016), and reduced dependence of a mutualist on partners (e.g., Kiers et al. 2007). We then compare how horizontal and vertical transmission determine which partners are transferred to the next generation and emphasize that both modes may lead to specialized or generalized interactions if partner breadth is heritable. Finally, we identify key areas in mutualism theory that niche concepts may help resolve.

A focus on cheaters and phylogenetically unrelated exploiters is common in many well-known mutualisms, including ant–fungus, cleaner–client–fish, legume–rhizobium, plant–arbuscular-mycorrhizal-fungi, and squid–*Vibrio* interactions (Ghoul et al. 2014, Jones et al. 2015). To explain why mutualisms are evolutionarily stable despite the potential for cheating, research has emphasized mechanisms that couple partner

fitnesses, either through repeated interactions (partner fidelity) or “preference traits” (partner choice or sanctions) that allow a focal mutualist to exclude cheaters and specialize on the most beneficial partner(s). Thus, both theory and empirical work has explored how partner fidelity can cause the condition or vigor of one partner to feed back to affect the condition or vigor of the other (Bull and Rice 1991, Weyl et al. 2010), and examined how mutualists may “choose” high-quality partners via screening (Archetti et al. 2011*a, b*), signaling (Grafen 1990, Batstone et al. 2017), morphological adaptations that spatially structure symbionts (Sachs et al. 2011), or preferential allocation of rewards (Kiers et al. 2003, 2011, Bever et al. 2009, Chomicki et al. 2016). However, recent studies have questioned whether cheating is as widespread in mutualisms as is often assumed (Friesen 2012, Jones et al. 2015, Frederickson 2017), and thus whether mutualists are really under selection to specialize on high-quality partners to avoid associating with cheaters (Frederickson 2013). The idea that indiscriminate mutualists might actually outperform choosy mutualists, especially in the face of environmental heterogeneity, is little explored in mutualism literature.

ENVIRONMENTAL HETEROGENEITY SHAPES PARTNER BREADTH

By bridging the concepts of mutualism evolution and niche breadth, we can explore how the environment shapes partner breadth within a more unified framework. Environmental variation impacts partner breadth indirectly through its effects on (1) partner availability, by determining which partners can persist, and (2) partner quality, by determining how beneficial a partner is relative to other potential partners in the community (or compared to no association at all). For example, broad partner breadth is not possible without a diverse partner pool. Similarly, specialization may evolve simply because there are few partners available in the local environment (e.g., Schleuning et al. 2012).

The environment arguably has the greatest capacity to shape the partner pool by influencing partner availability and performance in the free-living stage of symbionts (e.g., while rhizobia are in the soil), or during non-mutualistic life history stages in partners that are always free-living (e.g., environmental effects on early instars that will become pollinating insects as adults). Although vertically transmitted symbionts almost never live outside a host, most mutualisms are horizontally transmitted (Sachs et al. 2011) and thus subject to exogenous environmental filters.

Within a given partner pool, a specific partner’s quality is contingent on the abundance, proximity, and identity of other partners in the community (Howe 1984). If a higher-quality partner is temporarily absent, associating with any partner might be more beneficial than not forming any associations (e.g., Thomson 2003, Parker et al. 2016, Batstone et al. 2017). Heath and Stinchcombe (2014) describe how variation in partner quality can be generated by both spatial and temporal fluctuations in biotic or abiotic factors. By extension, such genotype-by-environment interactions for partner quality could favor generalist over specialist mutualists if the identity of the highest-quality partners varies across space or time (Howe 1984). Analogously, previous models of niche breadth evolution have illustrated how environmental variation influences whether specialization or

generalization should evolve (e.g., Thrall et al. 2007, Poisot et al. 2011, Forister et al. 2012, Sexton et al. 2017).

Acting on partner availability and relative quality, environmental variation can lead to broad partner breadth in two general ways. First, multiple partners may provide a cumulative benefit to the focal mutualist. For example, flexible mutualist-partner associations that change over time, mirroring the dynamic needs of the mutualist, may provide an advantage over static specialization (Thompson 2005, e.g., Palmer et al. 2010, Moeller and Neubert 2016). Alternatively, heterogeneous environments may favor mutualists with diverse partners if association with a broad range of partners increases breadth along another niche axis (e.g., water depth for corals; Silverstein et al. 2012). That is, mutualistic associations that vary through time or space may reflect adaptive responses to underlying environmental conditions, rather than indicating the mutualist’s failure to choose the best or exclude the worst partner. Second, certain environmental conditions may preclude selection for specialization and instead promote broad partner breadth indirectly, by either eroding variation in partner quality (e.g., when a high-quality partner in one environment carries a cost that reduces its relative benefit in another environment; Simonsen and Stinchcombe 2014) or reducing the dependence of mutualists on their partners, relaxing selection for choosy hosts (e.g., Kiers et al. 2007).

SELECTIVE ADVANTAGE OF BROAD PARTNER BREADTH

The cumulative benefits of multiple partners

The idea that biodiversity enhances ecosystem functions such as productivity, stability, and invasion resistance has a long history in community ecology (Tilman and Downing 1996, McCann 2000, van Ruijven and Berendse 2005). Here, we ask if key niche-based mechanisms from this literature, including sampling, complementarity, and portfolio effects (Loreau and Hector 2001, Figge 2004, Schindler et al. 2010, 2015), can explain why mutualists that associate with multiple partners may be selectively favored.

With a sampling effect, if partners vary in quality, then a more diverse sample of the partner community may be more likely to include the most beneficial one (Fig. 2A). Albrecht et al. (2012) documented a positive relationship between radish (*Raphanus sativus*) reproductive success and pollinator functional diversity. This relationship was largely driven by social bees, which were frequent floral visitors and contributed most to fruit set. The benefit of pollinator diversity to the plant was primarily a sampling effect; more functionally diverse pollinator assemblages were more likely to include social bees. To our knowledge, this is one of the only studies explicitly testing for a sampling effect in a mutualism. García and Martínez (2012) tested for a sampling effect after the fact, but found that complementarity more likely explains the positive relationship between frugivore diversity and seed dispersal, and other relevant papers are conceptual reviews, e.g., Schleuning et al. (2015). However, we expect sampling effects when the available partners perform the same function but vary substantially in their quality for a given host. Thus, we posit that sampling effects may be similarly important in other systems with known, marked variation in partner quality, such as in plant–pollinator systems beyond that of

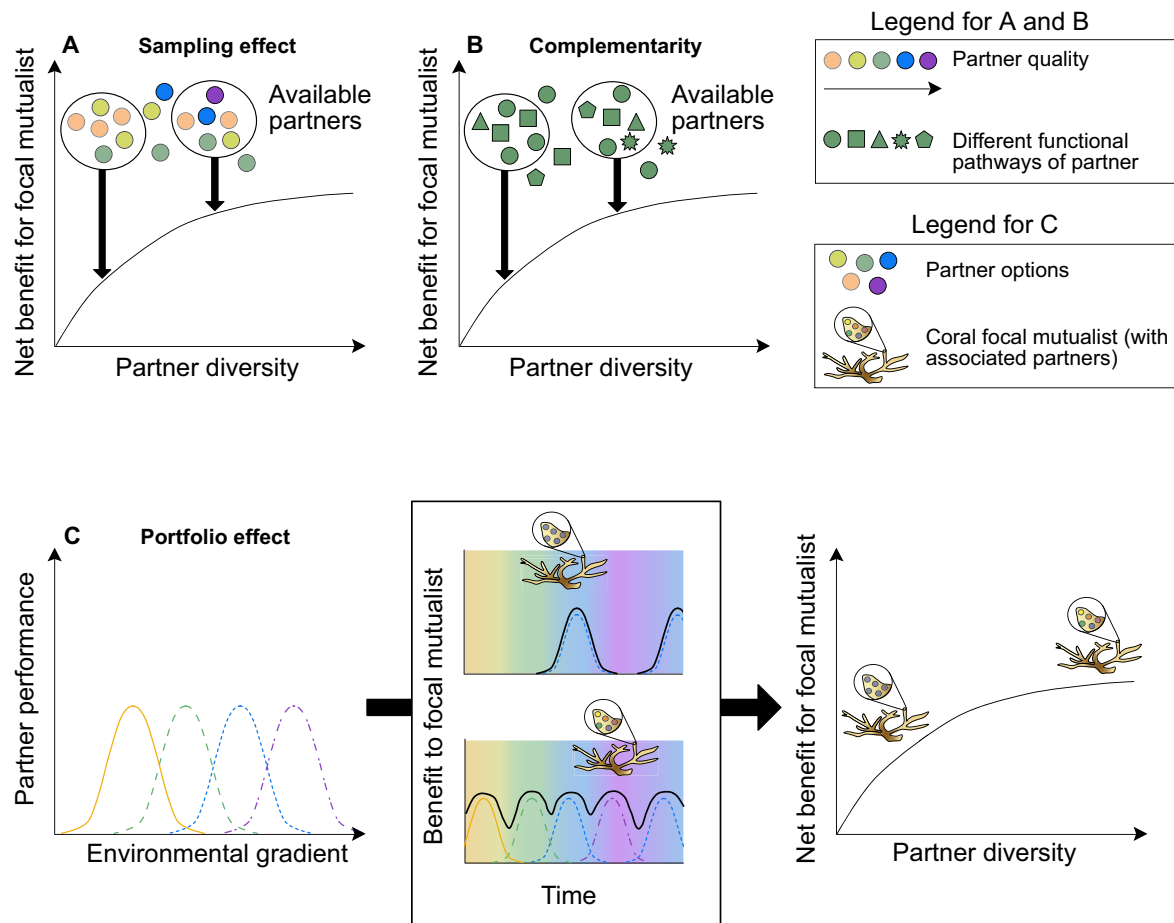


FIG. 2. Applying three theories from the biodiversity–ecosystem function literature to mutualism. Mutualists may benefit from associating with multiple partners if (A) it allows them to interact with the most beneficial partner because they “sample” more of the community; (B) partners perform similar functions through complementary pathways or mechanisms (i.e., niche partitioning); or (C) it stabilizes the benefit derived over time from a pool of partners with asynchronous dynamics or different performance optima and trade-offs.

Albrecht et al. (2012) or legumes that associate with multiple rhizobium strains. Similarly, *Vibrio* squid are initially colonized by multiple bacterial strains (a broad sampling of the symbiont community), but only the most cooperative strains survive (Nishiguchi et al. 1998). In general, the net benefit of sampling is likely to depend on the relative costs and benefits of sampling high- and low-quality partners.

In the biodiversity–ecosystem function literature, the joint presence of distinct functional groups, such as grasses, legumes, and forbs in a plant community, has repeatedly been found to increase ecosystem function through complementarity of functional groups (Cardinale et al. 2007). In a mutualism, if partners occupy different niches and provide the same type of rewards or services to a focal mutualist using different mechanisms or pathways, then generalist mutualists may benefit from complementarity among their partners (Fig. 2B). Stachowicz and Whitlatch (2005) found that two gastropod species that consume different invertebrates that foul the surface of the red alga *Chondrus crispus* provided complementary benefits, such that only the simultaneous presence of both gastropods left the alga free from fouling. Similarly, the glassy-winged sharpshooter (Auchenorrhyncha) associates with two bacterial endosymbionts with complementary amino acid synthesis pathways, such that the sharpshooter

must host both to obtain all amino acids necessary for survival (McCutcheon and Moran 2007).

Applying the diversity–invasibility hypothesis from invasion biology (Elton 1958, Levine and D’Antonio 1999) to mutualism also leads to the prediction that diverse partners may benefit a focal mutualist by preempting the establishment of exploiters or other antagonists. A prominent hypothesis for why human or other host-associated microbiomes often confer resistance to pathogens is that pathogens compete for space or resources with the benign microbiota; the more completely the benign microbiota fill available niches, the harder it may be for invading pathogens to establish (Costello et al. 2012). Moreover, a diverse microbiome may be more likely to contain key invasion-resistant species, or include microbes that interact to increase invasion resistance (Dillon et al. 2005, Piovia-Scott et al. 2017). By experimentally manipulating the species richness of microbes on the skin of frogs, Piovia-Scott et al. (2017) showed that a more diverse microbial community reduced frog susceptibility to the widespread pathogen *Batrachochytrium dendrobatidis*. They attributed the greater invasion resistance of more diverse microbial assemblages primarily to dominance effects, in which the bacteria best at combating the pathogen dominated in species-rich communities, and complementarity, in

which species-rich communities outperformed single species in terms of inhibiting pathogen growth.

Associating with multiple partners may also lead to more consistent returns through time if partner species exhibit different population dynamics or performance trade-offs (portfolio effect; Fig. 2C). In speciose communities, asynchronous species dynamics produce stability at the community level (e.g., Doak et al. 1998). Similarly, trait variation within species may stabilize population density over time (Bolnick et al. 2011). This diversifying bet-hedging is analogous to temporal niche complementarity. In the Albrecht et al. (2012) pollinator study, temporal niche complementarity of pollinators may also have increased plant seed set. Since stigmas are receptive only briefly and the timing of receptivity varies among plants, the authors proposed that the presence of pollinators foraging at different times improved pollination success. Several pollination studies also show how variation in partner availability determines the benefit of broad partner breadth through its impact on partner relative quality. Often, when a high-quality pollinator is unavailable, plants benefit from visits by low-quality pollinators (e.g., Thomson 2003, Parker et al. 2016), meaning that retaining the capacity to interact with both high- and low-quality pollinators can produce more consistent pollination. These studies demonstrate the benefits of broad

partner breadth when partner availability and quality varies temporally. Further, both complementarity and the portfolio effect rely upon niche partitioning among partners to explain how partner diversity increases the productivity or stability of a system (here, of rewards conveyed to the host).

Partners may also have complementary effects over time if the focal mutualist's needs change across ontogeny, resulting in a different "ideal" partner at different life stages (Howe 1984, Thompson 2005, Moeller and Neubert 2016). Mutualist ontogeny and the temporal sequence of interactions between a mutualist and its partners change the relative benefit of each partner (Barker and Bronstein 2016). Furthermore, because organisms are constrained by trade-offs in allocation, that is, a mutualist must apportion resources to its own growth, longevity, or reproduction, and to its partners, a mutualist's optimal allocation strategy may change through time. Even partners that appear to be detrimental at one time point may benefit a mutualist over the long-term. *Vachellia* (previously *Acacia*) *drepanolobium* associates with several ant species sequentially over its long life; the most aggressive ant species is effective at reducing herbivory but also sterilizes its host plant by destroying floral buds, while less aggressive ants provide less defense but do not inhibit host reproduction. When these associations occur in a particular order across the plant's ontogeny, each ant

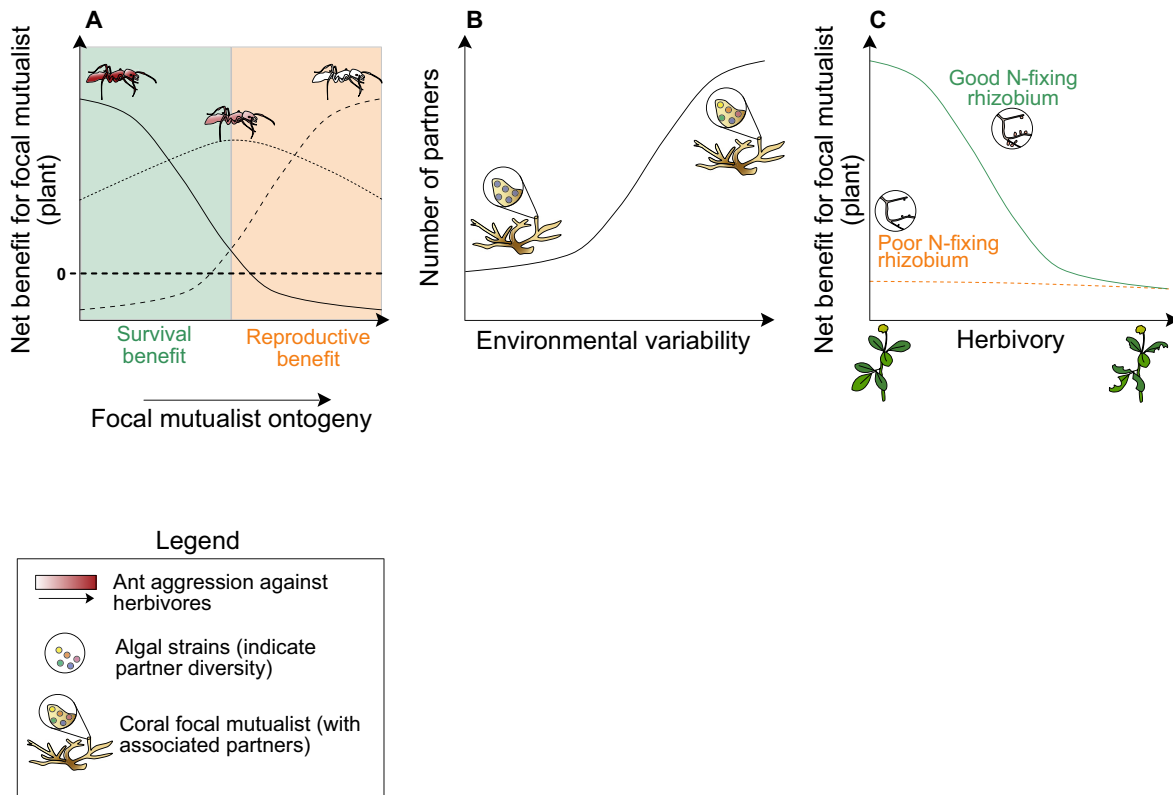


FIG. 3. Environmental variation influences mutualisms. (A) The most beneficial partner may change across host ontogeny (internal environmental variation). For example, an aggressive ant species deters herbivores but sterilizes the plant, reducing early reproduction but increasing survival (Palmer et al. 2010). Plants associating later in life with ants that do not deter herbivores may actually benefit, through a stress-induced burst of reproduction with little reduction in lifespan (Palmer et al. 2010). (B) Due to performance trade-offs of symbionts across environments, hosts should benefit from associating with a greater number of partners in more variable environments (Baker 2003). (C) External biotic conditions also shape the net benefit of different partners. For example, when herbivores are absent, the legume *Medicago lupulina* does best when it associates with effective nitrogen-fixing rhizobia; however, in the presence of herbivores, the performance benefit of good partners disappears, as nitrogen-rich plants are preferred by herbivores (Simonsen and Stinchcombe 2014).

species contributes positively to plant lifetime fitness (Fig. 3A; Palmer et al. 2010). Partnering with the sterilizing ant species early on reduces early reproduction but helps trees survive this vulnerable stage, whereas partnering late in life with less aggressive species allows mature trees that are more tolerant of herbivory to reproduce.

The same niche partitioning that allows different partners to perform complementary functions in space or time, thus providing greater or more stable rewards to a focal mutualist, may also explain the coexistence of multiple partner species in a community. That is, niche partitioning among mutualistic partners that provide the same type of reward (e.g., pollinators that forage at different times; Albrecht et al. 2012) may reduce competition among them and facilitate their coexistence. Moreover, niche partitioning within a host over ontogeny or due to spatial segregation of partners or different metabolic pathways could facilitate the coexistence of multiple partner genotypes that provide similar rewards. This contrasts with Thompson's (2005) "hypothesis of coevolved monocultures and complementary symbionts," which posits that hosts seldom associate with assemblages of functionally similar, potentially competing symbionts because of "intense selection on host populations to minimize the genetic diversity of a symbiont species."

Overcoming constraints along other niche axes

Broad partner breadth may also give mutualists an advantage if it increases their tolerance of other environmental conditions, but whether breadth along a given niche axis constrains, expands, or correlates with breadth along other axes remains an open question. Compared to no association, mutualism can expand a population's niche along other axes (Bruno et al. 2003, Poisot et al. 2011, Bulleri et al. 2016), such as when endophytes increase host drought tolerance (Afkhami et al. 2014b). However, it can also constrain a focal mutualist to living in conditions that its partners can tolerate (Peay 2016). For example, because of their fungi's cold susceptibility, fungus-growing ants could not expand northward until the fungi adapted to higher latitudes (Mueller et al. 2011). Similarly, seed dispersal by ants failed to expand the niche of the plant *Hexastylis arifolia* because of the ants' more limited tolerance to soil moisture conditions (Warren et al. 2010).

By associating with multiple partners that exhibit different performance optima along a niche axis (Fig. 2C), mutualists may overcome the constraints of any particular partner. More specifically, broad partner breadth may benefit a focal mutualist if a partner's ability to tolerate a stressful abiotic or biotic condition comes at the expense of its performance as a mutualistic partner. For example, the four ant species that defend the cactus *Ferocactus wislizeni* against herbivores are most active at different temperatures and exhibit thermotolerance–defense trade-offs; the best defender cannot withstand high heat, leaving only the most thermotolerant but least aggressive ant species to protect the cactus during the hottest part of the day (Fitzpatrick et al. 2014). Furthermore, mutualists might benefit more from associating with many partners that each provide maximal rewards under a different narrow range of environmental conditions, rather than by specializing on a single partner that tolerates

a wide range of conditions but performs more poorly. Therefore, when environmental conditions change across space or time, the presence of partners with different performance optima may lead to adaptive turnover of focal mutualist–partner associations.

Indeed, heat stress is known to alter partnerships between several genera of scleractinian coral and their algal endosymbionts (*Symbiodinium*). After heat stress events, the prevalence of thermotolerant algae has been shown to increase in certain coral–algal partnerships by two different mechanisms. First, corals associated with heat-sensitive algae may expel their algal partners ("bleach") at high temperatures and uptake new, more thermotolerant partners after bleaching (Sotka and Thacker 2005, Silverstein et al. 2015). In this scenario, turnover of focal mutualist–partner associations (rather than the coral's own acclimation) increases coral thermotolerance. Alternatively, the prevalence of thermotolerant algal partners may increase after heat stress events if coral preference or competition among partners alters dominance patterns within a coral's existing endosymbiont community (Little et al. 2004). These two different scenarios suggest contrasting patterns of partner breadth. Corals may have narrow partner breadth at each time point but be associated with a wide range of partners over time if novel partners are taken up after bleaching, whereas the other mechanism suggests that only the strength of associations (rather than the identity of the partners) changes over time.

Like other axes of niche breadth, partner breadth can be decomposed into multiple levels of biological organization (Bolnick et al. 2011). Thus far, we have considered partner breadth to be a heritable trait of a genotype that may evolve in a population. We have argued that individuals with genotypes allowing broad partner breadth may be better able to cope with temporal fluctuations in environmental conditions or with microhabitat heterogeneity. At higher levels of biological organization, variation among focal mutualists in partner associations within a population (e.g., flower color morphs visited primarily by different pollinator species) may produce broad population-level partner breadth (e.g., a diverse pollinator community visits the floral population as a whole; Stanton 1987) that can be maintained by fluctuating, frequency-dependent, or diversifying selection. Similarly, mutualists may associate with different partners across their geographic range, and this population-level differentiation among more specialized mutualists can produce wide species-level niche breadth (e.g., Afkhami et al. 2014b, Charlton et al. 2014). That is, selection for narrow partner breadth at the genotype level may still lead to broad partner breadth at the level of mutualist populations or species.

Continuing our coral example, at the population level, mortality of hosts associating with less tolerant partners can increase the proportion of corals associating with thermotolerant strains after bleaching. At the species level, coral–algae associations of a widely distributed coral turn over in a predictable way along a water depth gradient; corals at shallow depths (where conditions vary spatially and temporally) associate with algae from multiple clades, whereas deep-water corals (that experience uniform conditions) partner predominantly with a single distinct algal clade (Baker 2003, Fig. 3B).

More generally, broad partner breadth at the species level may result from local coadaptation, if mutualists perform best when paired with local partners (e.g., Mueller et al. 2004, Johnson et al. 2010, Porter et al. 2011, Ehinger et al. 2014, Rúa et al. 2016), and partners perform best with native mutualists (Bever 1999). Local coadaptation should result in narrow individual- or population-level partner breadth, but broad partner breadth across the geographic range of a species. Local coadaptation may result from both the focal mutualist and its partner(s) independently adapting to their local environment, or to each other (Thompson 1999, 2005, Poisot et al. 2011). In the latter case, traits that act like lock-and-key mechanisms, such as molecular signaling between legumes and rhizobia or the domatia openings of the ant-plant *Leonardoxa africana* and the head shape of domatia-dwelling ants, may facilitate partner recognition and specificity (Brouat et al. 2001, Reinhardt 2007, Wang et al. 2012).

We have suggested that associating with diverse partners may increase a mutualist's niche breadth along other abiotic or biotic axes, but it is also possible that mutualists occurring across a wide range of environments encounter a greater diversity of partners, and thus, have broader partner breadth (i.e., a reversed causal relationship; see Fort et al. 2016). Similarly, mutualists with limited niche breadth might associate with few partners by default. Thus, mutualisms might appear specialized, but this specialization could result from each partner being specialized on another niche axis, rather than on each other. Experiments quantifying environmental tolerances of mutualists with and without partners would help to evaluate these competing hypotheses (Peay 2016).

LACK OF SELECTION FOR NARROW PARTNER BREADTH

Even when associating with multiple partners does not provide a clear benefit to a focal mutualist, selection may not favor specialists, particularly when environmental conditions reduce variation in quality among partners, lower the costs of low-quality partners, or alleviate the dependence of focal mutualists on partners.

The availability of multiple partners that vary in quality is a prerequisite for the evolution of preference traits like partner choice; when the available partners are all of similar quality, mutualists should not be picky (Bull and Rice 1991, Noë and Hammerstein 1994, but see Batstone et al. 2017). If partner populations are highly structured, such that partner variation is largely among mutualists rather than within an individual mutualist's local sphere of influence, individual mutualists will have little variation on which to exert selection (Akçay 2017). For example, rhizobia and mycorrhizae are likely more patchily distributed in unmanaged soils than in tilled agricultural soils (Kiers et al. 2002), and selection on a plant's ability to discriminate between high- and low-quality partners may thus be weak or absent under natural soil conditions. Moreover, variation in partner quality that is observable under other conditions might also be masked by the presence of a third party. In a field experiment, the presence of herbivores determined whether legumes with effective rhizobia outperformed legumes that had also been inoculated with an "exploiter" rhizobia strain that does not fix nitrogen (Simonsen and Stinchcombe 2014); the benefit of effective rhizobia observed when herbivores were excluded vanished

when herbivores were present, because insects preferentially consumed the nitrogen-rich leaves of plants with nitrogen-fixing rhizobia (Fig. 3C).

If partner benefits saturate quickly and a mutualist achieves the maximum benefit possible with only a few high-quality partners, then the opportunity cost of associating with low-quality partners might be reduced or even eliminated (Archetti and Scheuring 2011, 2013, Moeller and Neubert 2016). In other words, environmental conditions that consistently maintain a sufficient number of high-quality partners may preclude selection for narrow partner breadth, even if low-quality partners are present. For example, the legume *Trifolium pretense* performed similarly when inoculated with a mixture of both high- and low-quality arbuscular mycorrhizal fungi as when inoculated with only the high-quality partner, despite being equally infected by both strains (Argüello et al. 2016).

In addition, interactions among partners may reduce exploitative behavior and therefore the potential costs of associating with an uncooperative partner. Cleaner fish may exploit client fish by consuming tissues of the client fish rather than removing unwanted epibionts; however, when client fish interact simultaneously with multiple cleaner fish, tissue consumption by one cleaner can negatively affect the fitness of the other interacting cleaners, potentially leading to greater cooperation as cleaners keep one another in check (Gingins and Bshary 2015). Therefore, limiting associations to one or a few partners may not be advantageous even when low-quality and potentially exploitative partners are present.

Alternatively, if focal mutualists do not depend strongly on the benefits provided by partners, there may be little selection to specialize on the best partner. For example, in productive environments, the biological constraints that lead to specialization (e.g., in diet requirements) may be relaxed, promoting greater generalization (Poisot et al. 2011). Nutritional mutualisms may be particularly sensitive to anthropogenic nutrient addition, as human activities increase the availability of resources once provided more exclusively by mutualistic partners (Shantz et al. 2016). Legumes adapted to high- compared to low-nitrogen soil conditions associate more frequently with less beneficial rhizobia (Weese et al. 2015, Klinger et al. 2016), perhaps because limiting associations to the 'right' partner is less important when soil nitrogen is not limiting (Kiers et al. 2007). However, previous frameworks actually predict the opposite: if biotic complexity (e.g., the number of potentially interacting partner genotypes) correlates positively with resource availability (e.g., nitrogen), then a focal mutualist should be more selective to avoid ineffective partners (Bever 2002, Thrall et al. 2007). Measuring how the diversity of a focal mutualist and its partners shifts across a resource gradient would indicate whether there is greater or reduced specialization under high resource conditions. In sum, hosts may associate with a broad array of symbionts not only because of a selective advantage to generalize, but also because some environmental conditions preclude selection for specialization.

PARTNER BREADTH AND TRANSMISSION MODE

Vertical transmission is generally thought to involve narrower partner breadth than horizontal transmission (Douglas 1998). However, either transmission mode may lead to

specialized or generalized interactions; horizontal transmission may still result in narrow partner breadth if the environmental conditions favor the evolution of specialization, while vertical transmission may still lead to broad partner breadth if multiple partners are transmitted simultaneously (e.g., when infants acquire a diverse gut microbiome from their mother's breast milk; Collado et al. 2009).

Furthermore, each transmission mode confers different benefits depending on the environment: when partners are scarce, vertical transmission assures that mutualists and their offspring will have partners, allowing mutualism to persist, while horizontally transmitted mutualisms may be lost (e.g., Chomicki and Renner 2017b). In contrast, in environments where compatible partners are widely available, horizontal transmission may provide mutualists with the flexibility to acquire locally adapted partners. Combining aspects of both transmission modes (i.e., mixed transmission) may therefore be adaptive when partner availability is unpredictable (Vrijenhoek 2010). Indeed, many examples of mixed transmission are known (reviewed in Ebert 2013), involving both active transfer of symbionts from parent to offspring and more indirect means of symbiont transmission. Female beewolves, although they acquire multiple symbionts from the environment, actively transfer only the preferred strain of antifungal bacteria *Streptomyces* to their offspring (Kaltenpoth et al. 2014).

Alternatively, offspring may inherit partner breadth, rather than specific partners, from their parents in two ways: partner breadth may be heritable or a parent's partner breadth may influence the composition of the local partner pool, potentially affecting offspring if dispersal is limited. In the squid–*Vibrio* symbiosis, squid hosts actively expel high-quality symbionts into the water column, effectively “seeding” the local environment with these symbionts for nearby juvenile squid to acquire (Lee and Ruby 1994, Nyholm and McFall-Ngai 2004). Last, focal mutualists that alter partner availability may impact not only partner breadth of subsequent generations, but also that of other mutualistic species within the community, analogous to the kind of niche construction and ecological inheritance described for abiotic niche axes (Odling-Smee et al. 2003, Erwin 2008). Therefore, rather than dichotomous categories, vertical and horizontal transmission can be placed on a gradient reflecting the degree to which the available partner pool is shaped by past or current partner breadth.

FUTURE DIRECTIONS

How can we test for sampling, complementarity, and portfolio effects of partner diversity in mutualisms?

As we have seen, biodiversity–ecosystem function theory has been tested in a few mutualisms but has yet to become fully integrated with the mutualism literature. This may be, in part, because much early mutualism research focused on pairwise interactions; however, as more studies consider diverse communities of partners (e.g., in pollinators; Fründ et al. 2013, Pisanty et al. 2016), these niche-based theories can be increasingly used to understand patterns of mutualistic associations. Approaches used to tease apart the different contributions of diversity to ecosystem function should be

directly transferrable to studies of mutualisms. For example, the additive partitioning approach proposed by Loreau and Hector (2001) for parsing complementarity from sampling effects would require measuring how well a focal mutualist performs with each partner in isolation and with a community of partners, as well as the contribution of each partner to mutualist performance.

How do different partner niche axes interact?

Many focal mutualists interact not only with multiple partners that confer similar rewards, but with multiple partners that provide very different rewards or services, such as a plant that interacts with defensive ants, pollinators, seed dispersers, and beneficial microbes (Stanton et al. 2002, Lau and Galloway 2004, Ness 2006, Cahill et al. 2008, Larimer et al. 2010, Afkhami et al. 2014b). Mutualists may exhibit narrow breadth for one partner type but broad breadth for another, and participation in one type of mutualism may influence another. For example, disruption of a belowground plant–fungal symbiosis led to a shift in the plant's pollinator community from large to small-bodied bees (Cahill et al. 2008). A network study of plant interactions with pollinators, seed dispersers, and ant bodyguards suggested different partner breadths among mutualism types (Dáttilo et al. 2016). None of the focal plant species participated in all three types of mutualism, and of the few plant species engaging with multiple types of partners, certain combinations of interactions were more common than others (e.g., ant-defended plants were never bird-dispersed). Future research that continues to examine how the breadth of partners conferring one type of reward or service affects the breadth of partners offering different benefits would further develop our understanding of mutualist–partner associations.

How does shared evolutionary history affect partner breadth?

When a mutualist arrives at a new site, it might benefit from broad partner breadth, as this trait increases the likelihood of associating with compatible partners despite the absence of shared evolutionary history (Bascompte 2009), much like the sampling effect. Over evolutionary timescales, however, transitions from generalization to specialization are supported by numerous phylogenetic studies (e.g., Gilbert and Webb 2007, Vamosi et al. 2014, Chomicki and Renner 2017b), that show partner breadth is more likely to narrow than broaden. Ancestral host lineages may exhibit broader partner breadth compared to derived lineages if traits that lead to specificity (e.g., signaling-recognition systems) tend to be more derived. For example, the symbiosis between chemoautotrophic bacteria and heterodont bivalves tends to be more generalized within the more basal bivalve lineages and more specialized within more derived bivalve lineages (Distel 1998, Vrijenhoek 2010, Batstone and Dufour 2016).

Coevolution among focal mutualists and partners may also drive specialization in one partner. That is, broadening the breadth of one partner actually causes the narrowing of the other (Chomicki et al. 2017a), potentially explaining why specialization is often asymmetric in mutualistic networks (Thompson 2005, Bascompte et al. 2006). For example, as the Sword-billed Hummingbird (*Ensifera ensifera*) utilized a

greater number of food plant species, the plants became more specialized to accommodate the Hummingbird's long bill (Abrahamczyk et al. 2014). More generally, whether specialization within mutualism is an evolutionary dead-end depends on the specific mutualist-partner association in question and the degree to which specialization increases extinction, especially if reversal to autonomy or partner switching is not possible (Chomicki and Renner 2017b, Chomicki et al. 2017a). Whether we should generally expect a shift from broad to narrow niche breadth over evolutionary time is likely contingent on the type of mutualism and the diversity of partner taxa that can potentially interact.

How do we reliably quantify partner breadth?

All of the above questions rely on having estimated partner breadth, but doing so can be challenging. The number and identities of partners with which hosts typically associate are well documented in some mutualisms (e.g., certain well studied plant-pollinator systems), but in other mutualisms (e.g., bacterial symbiosis), even defining a species or strain can be challenging. Changes in partner breadth across scales further complicate niche breadth measurement, as mutualists' biotic specialization may be reported as an aggregate measure at the species level, or generalized from observations on one or few populations. Mutualistic networks have provided data on species-level partner breadth, and are starting to reveal the interplay among multiple mutualisms (Dáttilo et al. 2016), but networks constructed at the genotype (rather than the species) level are needed to further our understanding of niche breadth evolution.

CONCLUSION

In summary, we have described how the environment shapes both partner availability and relative quality, thus influencing a mutualist's partner breadth, and we have outlined the factors predicted to lead to selection for generalization or to preclude selection for specialization within mutualisms. Although mutualists are often expected to be choosy to avoid associating with cheaters, we propose that viewing mutualisms in light of niche breadth and other community ecology theory helps us understand why generalization is often adaptive in mutualisms. There is a pressing need for future work that quantifies partner breadth across a wide range of systems and scales in order for us to fully appreciate the resiliency of mutualistic interactions in the face of environmental change.

ACKNOWLEDGMENTS

All authors conceived the ideas. R. T. Batstone and K. A. Carscadden contributed equally to the manuscript; both co-wrote and edited the manuscript, while K. A. Carscadden designed the figures. M. E. Afkhami and M. E., Frederickson provided guidance and substantial edits on each draft. For their insightful input on the manuscript, we thank G. Chomicki and an anonymous reviewer, as well as members of the Frederickson Lab (S. Meadley Dunphy, J. Laurich, K. Kaur, and M. Trychta), Emery Lab (N. Emery, R. La Rosa, A. Panetta, and C. Van Den Elzen), and M. Cadotte. We acknowledge the following funding sources: NSERC Discovery Grant (M. E., Frederickson), University of Miami (M. E. Afkhami), Ontario Graduate Scholarship (R. T. Batstone), the University of

Toronto (M. E., Frederickson, R. T. Batstone), and the University of Colorado Boulder (K. A. Carscadden).

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