

Research on mutualisms between native and non-native partners can contribute critical ecological insights

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Abstract

Mutualisms are important structuring forces in ecological communities, influencing ecosystem functions, diversity, and evolutionary trajectories. New interactions, particularly between native and non-native species, are globally increasing in biotic communities as species introductions accelerate. Positive interactions such as novel mutualisms can affect the fitness of organisms in invaded communities. Non-natives can augment native mutualism networks, replace extinct native partners, or disrupt native mutualisms. Because they are actively forming or newly formed, novel mutualisms offer a unique opportunity to examine in real time the factors governing early mutualism formation and stability, including frequency-dependent processes and those relying on specific traits or functions. These central ecological questions have been inferred from long-formed mutualisms, but novel mutualisms may allow a glimpse of successes and failures in ecological time with insights into the relative importance of these factors as ecological systems shift. To this end, this commentary addresses how novel mutualisms inform our understanding of mutualism formation, stability, the importance of functional traits, and niche vs. neutral processes, using examples across multiple systems. Novel mutualism research thus far has been largely limited in both questions and ecosystems, but if more broadly applied could benefit both theoretical and applied ecology.

Keywords

Positive interactions, marine, belowground, biological invasions, non-native species, novel mutualisms

Introduction

Mutualisms as important structuring forces

Mutualisms are thought to be ubiquitous across habitat types (Bronstein et al. 2004), driving trait evolution and structuring ecological communities (Bruno et al. 2003; Bronstein et al. 2006). Participating species offer and receive currencies such as protection, nutrients, or transportation. Individual species often interact with multiple partners, creating complex mutualistic networks that can confer resilience to species losses through partner redundancy (Aizen et al. 2012). Mutualisms are now recognized as fundamental to ecological complexity and stability (Montoya et al. 2006).

Ecologically and evolutionarily, mutualisms have shaped many biological invasions and vice versa (recently reviewed by Traveset and Richardson 2014). The importance of mutualisms in facilitating invasion and the potential for mutualism evolution to change as a result of biological invasions are critical areas of study (Kiers et al. 2010; Traveset and Richardson 2014). However, the formation of “novel mutualisms” between native and non-native species also serves as a remarkable opportunity to study the processes governing mutualism formation, failure, and fitness implications. As they become established in ecological communities, non-native species may enter mutualistic networks, potentially altering community dynamics and ecosystem functions (Traveset and Richardson 2014). Fundamental research in ecology has centered on the role of mutualisms in emergent ecosystem properties—that is, how mutualism formation, structure, and stability may have generated the species combinations and interactions observed in ecosystems today. Since this research concentrates on past processes, it is largely inferential, attempting to reconstruct likely pathways and thereby better understand ecosystem function. Two key areas of study include: 1) mutualism formation and stability in the context of partner cheating, opportunism, and partner extinction (Bronstein et al. 2006); and 2) how species’ traits and functions may or may not have predisposed them to participating in mutualisms (e.g., Janzen 1985). This latter line of inquiry examines, in essence, which comes first: participation in mutualisms or the traits that predispose participation, attempting to sort neutral opportunism from niche processes. Novel mutualisms provide an opportunity to examine these critical ecological questions from the opposite end of the process timeline: researchers can examine mutualisms as they form or fail, including the importance of functional traits, niche and neutral processes, and their stability over ecological time.

Because it focuses on early mutualism stages (rather than inferences from later stages), novel mutualism research may improve our understanding of the foundation for mutualisms more generally as well as the implications of potential mutualist introductions. This commentary uses specific examples of novel mutualisms to discuss early mutualism formation and stability, the role of functional traits, and niche vs. neutral processes in community assembly. Novel mutualism research to date has been heavily concentrated in the realms of invasion biology and aboveground, terrestrial ecosystems. We deliberately discuss traits of novel mutualisms across ecological domains to seek broad patterns relevant to these new avenues of research.

A useful definition

Scientific literature uses a variety of definitions for the term “mutualism.” The simplest, conventional definition for mutualism is any interaction between two species that results in fitness benefits for both species (notated as “+/+”) (Bronstein 1994b). This contrasts with antagonistic relationships in which one species benefits and the other is harmed (predation, parasitism, competition: “+/-”) and commensal relationships in which one species benefits while the other is unaffected (“+/0”) (Bronstein 1994b). Examples throughout this commentary reflect this definition of mutualism, although we acknowledge that interactions that encompass facilitation or other indirect benefits may represent nascent points from which more traditional mutualisms may arise.

Box 1. Glossary of terms describing interspecific interactions.

Mutualism: an interaction wherein both sides derive fitness benefits and the interaction occurs at the individual level (“+/+”).

Facilitation: an interaction wherein at least one species derives a fitness benefit and the other side is not detrimentally affected.

Obligate: an interaction necessary for survival of one or both of the species involved. (Antonym: Facultative)

Specific: an interaction in which a species has only a single partner or very small number of partners. (Antonym: General)

Diffuse: an interaction involving many species or a network. (Antonym: Pairwise)

Novel mutualisms as examples of early mutualism formation

Basic evolutionary and ecological research focused on emergent ecosystem properties has explored the factors driving mutualism formation. Benefits of mutualisms can be contextual (Bronstein 2001; Hay et al. 2004), leading to questions about the circumstances and strength of selection required for mutualisms to form (Sachs et al 2004; Foster and Wenseleers 2006) and persist. Species that form novel mutualisms must either be 1) initially capable of surviving and reproducing without mutualism (facultative) or 2) interactors that can form new, necessary mutualisms with little regard for partner identity (generalist) (Brodie et al. 2014). Species requiring mutualism to survive or reproduce may fail to recruit in a new ecosystem early in the invasion process, before novel relationships can develop (Fig. 1; Theoharides and Dukes 2007; Richardson and Pyšek 2012). Consistently, most examples of novel mutualisms are both facultative and generalist (Traveset and Richardson 2014). This parallels our contemporary understanding of most native-native mutualisms (Blüthgen et al. 2007).

Thus, novel mutualisms appear to recapitulate a general mutualism tendency to be facultative, particularly early in the mutualism formation process. Known facultative novel mutualisms include most novel seed dispersal relationships (e.g., Lenda et al. 2012), ant-plant and ant-insect mutualisms (Ness and Bronstein 2004), and a single example of a novel cleaning relationship: ectoparasite removal from non-native cows, *Bos javanicus*, by native birds, *Corvus orru* (Bradshaw and White 2006). Many invasive

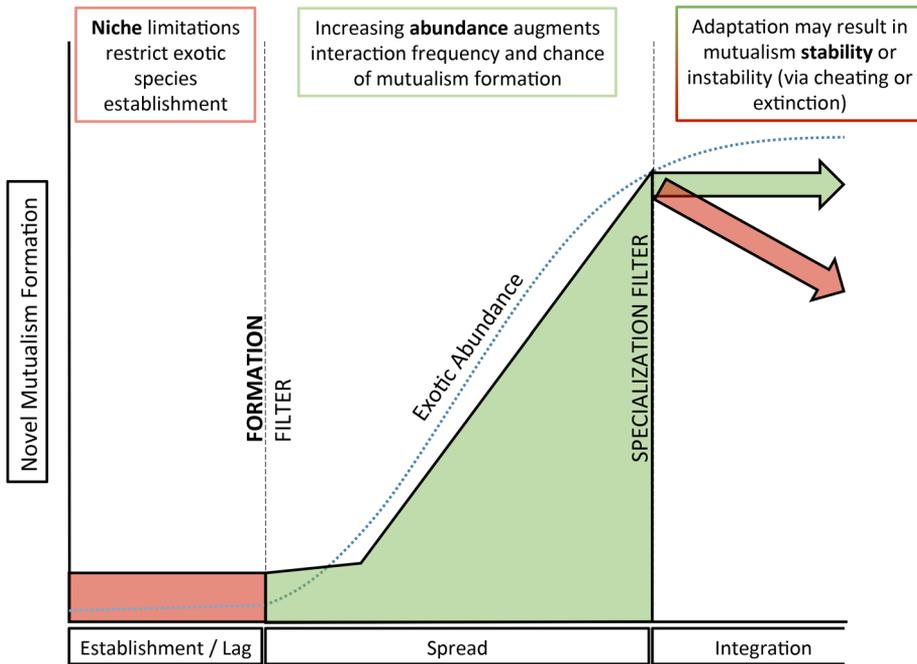


Figure 1. Conceptual figure of the formation and stability of novel mutualisms by niche and neutral processes at different stages of invasion. The x-axis represents three general stages of a biological invasion as necessary for mechanistic purposes, despite substantial debate in the literature about how invasion stages should be delineated. The y-axis represents the formation of novel mutualisms and the dotted line represents the shifting relative abundance of the non-native species. Red areas represent limitation of novel mutualism formation by the process described; green areas represent enhancement or reinforcement by the process described. Hashed vertical lines represent filters: the mutualism formation filter may be imposed by functional traits in the non-native organism or by niche traits preventing mutualism formation. Once the mutualism has formed and the species has spread, mutualism specialization filters may be imposed by strong selection for certain mutualistic traits; increased specialization may impact mutualism stability.

plants appear to be self-compatible or able to reproduce vegetatively, making animal-mediated pollination facultative in these cases (Burns et al. 2011). There are, however, exceptions: several aggressive invasive plants, such as purple loosestrife (*Lythrum salicaria*), Amur honeysuckle (*Lonicera maackii*), and multiflora rose (*Rosa multiflora*), differ from this pattern and demonstrate a stronger dependence on pollinators, partnering with generalist species during establishment (e.g., Jesse et al. 2006). Belowground, formation of novel associations between plants and soil microbes still occur readily (Traveset and Richardson 2014), despite the reduction of benefits in some cases. For example, non-native and native legumes in a Mediterranean shrubland formed partnerships with non-native rhizobia, despite the fact that benefits for native plants from the association were far below those typical of native rhizobial associations (Rodríguez-Echeverría et al. 2012). Similarly, the evolution of reduced mycorrhizal dependency of non-native plants

is evident from field data drawn from different populations of the same plant (Seifert et al. 2009). A notable exception is ectomycorrhizal (EcM) plants invading ecosystems in the Southern hemisphere that rely on mycorrhizas to establish and spread (Richardson et al. 2000). The complementary dependence of non-native soil biota on native host mutualisms is poorly studied. Most soil mutualists (e.g. mycorrhizal fungi, rhizobia, etc.) must form associations to complete their life cycle, although benefits from novel associations for the few EcM species studied may be reduced (Vellinga et al. 2009).

To our knowledge, there are only two documented examples of novel mutualisms in marine systems. One such novel marine mutualism is also facultative. The native sediment dwelling polychaete *Diopatra cuprea* in the mid-Atlantic U.S. incorporates the invasive red alga *Gracilaria vermiculophylla* into its decorated tube caps (Thomsen and McGlathery 2005). The non-native alga is also found unattached, but the stable attachment point of *Diopatra* tube caps increases its longevity and growth rate (Thomsen et al. 2009) and biomass (Byers et al. 2012). Although the nature of the reciprocal benefits of *G. vermiculophylla* to *D. cuprea* have not been investigated, *D. cuprea* generally receives shelter and food from the algae it hosts and favors attaching *G. vermiculophylla* over other native algal species (Thomsen and McGlathery 2005). The other, newly-discovered marine novel mutualism involves a non-native zooxanthella that partners with corals in the Caribbean, with mixed fitness implications: the novel partnership results in increased heat tolerance but reduced calcification for the native partners (Pettay et al. 2015).

Does the lack of other marine examples of novel mutualisms arise from a dearth of research or from a true lack of novel mutualism formation? The few other relevant research attempts in marine systems have failed to detect novel mutualisms. For example, an unusual zooxanthella found in a native Hawaiian coral, once considered a novel mutualism, is instead of cryptogenic origin (LaJeunesse et al. 2008). A search for novel coral-endosymbiont mutualisms in Jamaica was fruitless, despite a high probability of detection due to both the long-term establishment of an Indo-Pacific non-native coral and its common acquisition of endosymbionts by horizontal transfer in its native range (LaJeunesse et al. 2005). Observations of the invasive lionfish, *Pterois volitans*, loitering at reef cleaning stations throughout its invaded range in the Caribbean appear to be the behavior of a sit-and-wait predator (Côté and Maljkovic 2010) rather than the formation of a novel mutualism. In spite of these notable absences, however, a considerable increase in marine novel mutualism research is needed before it will be possible to conclude that the formation of novel marine mutualisms is rare and to consider the implications of such rarity for marine mutualism formation. Observation of this research gap may in itself increase awareness and detection.

Informing our understanding of mutualism stability using novel mutualisms

Research on novel mutualisms may also help us understand why some early mutualisms fail while others result in long-term associations. A focus of mutualism stability research is partner fidelity in the presence of “cheaters” (Ferriere et al. 2002). When cheating

predominates, mutualisms can become parasitic, with only one partner benefiting (Bronstein 1994a). Mutualism networks containing “cheating” partners, however, may occur only when beneficial partners are also present (Weyl et al 2010). Species that are generalist, partnering with many mutualistic partners, are likely to obtain mutualistic currencies from some partners, and thus to continue to participate in mutualisms even in the presence of cheaters. Mutualism stability is also a consideration when mutualisms become more specialized or obligate over time and partners are at risk of extinction (Thébaud and Fontaine 2010). Once again, mutualism stability may be enhanced by generalist partnerships, wherein each species has multiple partners so loss of a specific partner carries reduced impact. Mutualism specialization can evolve when fitness enhancements offset the enhanced probability of mutualism disruption (Schemske and Horvitz 1984). As early stage mutualisms, novel mutualists may derive lower levels of benefit on a per-mutualistic-interaction basis, but could be more stable than native mutualisms that have formed over a longer timeframe and more commonly exhibit specialization and cheating.

Since generality logically confers increased stability and reduces dependence on cheating or at-risk partners, it is unsurprising that mutualism network literature has demonstrated that generality is extremely common (e.g., Bascompte and Jordano 2014). Certain non-native mutualists appear to take this generality to an extreme, acting as “super-generalists” in novel mutualism networks (Olesen et al. 2002). Studies focused on individual species and their interactions have similarly detected high generality in novel mutualisms. For example, non-native ants that have been reported to partner with native plant species are generalists interacting with a wide variety of species across a global range (Ness and Bronstein 2004). Tending mutualisms between introduced ant species and native aphids are often similarly diffuse, with each ant species interacting with a number of aphid species (Ness and Bronstein 2004). Non-native species acting opportunistically can be generalist mutualists under some contexts and cheaters under others; the non-native Japanese white-eye (*Zosterops japonicus*), for example, nectar-robs some endemic Hawaiian plant flowers but pollinates others (Aslan et al. 2014). Recent evidence that Douglas fir (*Pseudotsuga menziesii*) invading New Zealand can readily form mutualisms with a diversity of native ectomycorrhizal fungi (Moeller et al. 2015) runs counter to other ectomycorrhizal invasive plants in the Southern hemisphere whose associations appear restricted to cosmopolitan or co-invading fungi (Nuñez et al. 2009; Dickie et al. 2010; Bogar et al. 2015). While no research has explored the network impact or stability of these interactions, we can logically predict that diverse associations may enhance stability.

Using novel mutualisms to improve our understanding of the importance of functional traits in community composition

Classic research on mutualism formation and stability also quantifies traits of mutualistic partners as potential limiting reagents that have led to the mutualisms present today. Functional traits form the foundation of many mutualistic networks. For exam-

ple, pollination syndromes and functional groups of effective partners can generally be defined by flower morphology, color, and reward type of a plant species (Fenster et al. 2004). Additionally, mutualisms appear to underlie the evolution of remarkable traits (Bronstein et al. 2006) such as unique morphologies and behaviors, effectively expanding the trait-space of a community. New understanding of major ecological processes, such as community assembly and environmental gradient effects, has come from taking a trait-based approach (McGill et al. 2006; Kraft and Ackerly 2014). Examining novel mutualisms through this lens has the potential to be especially revealing about the role of positive biotic interactions in community assembly (Sargent and Ackerly 2008), but this type of approach has thus far primarily investigated the prevalence of negative biotic interactions like interspecific competition and natural enemies.

How then, do newly arriving non-native species fit into an existing landscape of functional traits and functional group partnerships within a community? Trait-based methods can distinguish environmental filtering and community-level niche partitioning (Kraft et al. 2008). Under environmental filtering, trait-space should be constrained within a locale relative to that of the regional species pool, whereas community level niche partitioning occurs when traits are more evenly spaced than would be expected by chance due to interspecific competition (Kraft et al. 2006). If assembly rules are general, non-native species should, in the aggregate, pack accordingly into an environmentally constrained trait-space and/or exhibit divergent traits that may permit the filling of empty niches. Studies provide support for these processes (Ordonez et al. 2010; Tecco et al. 2010). In agreement with niche partitioning, species may be more likely to be invasive if they are functionally distinct from the native community and thus able to occupy vacant niches or possess novel weapons (Callaway et al. 2004). On the other hand, sheer propagule pressure (the abundance of the non-native species) has also been shown to underlie invasiveness (Lockwood et al. 2005).

In contrast to interspecific competition, a strong effect of mutualism on community assembly would select for non-native species with traits that link easily into existing mutualism networks, effectively favoring species that have traits more similar to native mutualists (Fig. 1). Such a signature of positive interactions has been detected in native communities of animal-pollinated plants, in which plants in the family Asteraceae benefit from the pollinator attraction of nearby individuals of closely related species (Sargent et al. 2011). Successfully established non-native species often demonstrate traits that facilitate their entry into existing interaction webs. Among non-native plants, animal-dispersed species include many with fleshy fruits such as berries and drupes that are widely appealing to a diversity of native disperser species (Aslan and Rejmánek 2010). Plant families known for high invasive tendencies tend to have open, accessible, and radially symmetrical flowers (e.g., Asteraceae), able to participate in generalist mutualisms and to partner readily with local pollinators in any given region (Traveset and Richardson 2006). Among non-native animals, highly successful mutualists include seed dispersers, which tend to be generalist feeders able to take ready advantage of available fruit resources (e.g., Foster and Robinson 2007). In most cases, such species join existing suites of seed dispersers to enter diffuse networks of seed dispersal (Aslan

and Rejmánek 2010). Most invasive plants also readily form belowground symbioses, despite the fact that not providing resources to soil biota should give invaders a distinct advantage (e.g. *Brassica* spp., Traveset and Richardson 2014). Interestingly, reduced mycorrhizal dependency of *Hypericum perforatum* in its invaded range is strongly correlated to specific changes in root architecture (Seifert et al. 2009). However, it is unclear whether other functional traits generally predispose non-native species to novel belowground mutualisms. Novel mutualisms offer the opportunity to describe the nature of the community filter at the front end of the mutualism formation process (Fig. 1).

The role of neutral and niche processes in novel mutualisms

As incipient partnerships, novel mutualisms also offer a unique opportunity to assess the relative importance of interaction frequency as driven by abundance, a neutral process, with that of adaptive traits that provide specific mutualistic benefits defined by the niches of their potential partners (Kaiser-Bunbury et al. 2014). This comparison is particularly valuable given the rapid increase in abundance of non-native species that become invasive, and the relative importance of these two mechanisms may be dictated by the particular stage of spread of a non-native species (Fig. 1).

The importance of niche and neutral processes in novel mutualisms could change during the invasion process as a non-native species initially establishes at low density, spreads and often increases in abundance, and ultimately is integrated into the community. As outlined above, non-native species requiring specific mutualisms are unlikely to establish because they may not find suitable partners. This limitation is largely niche-based. After establishment, non-native species that become problematically invasive may be present at much higher abundance than native partners. While an abundant non-native can reduce the stability of native mutualisms (Aizen et al 2008; Kaiser-Bunbury et al. 2011), high abundance also increases the frequency with which native mutualists encounter non-native species rather than native species, increasing the number of chances for a novel mutualism to form. For example, severe invasions by knapweed (*Centaurea stoebe*) and leafy spurge (*Euphorbia esula*) provide abundant hosts for native AM fungi, ultimately increasing mycorrhizal abundance and diversity (Lekberg et al 2013). Likewise, heavy infestations of yellow starthistle (*Centaurea solstitialis*) represent a large resource visited by a wide diversity of native pollinators (McIver et al. 2009). If the relative abundance of these non-natives remains high, native species that are able to gain benefit from novel partnerships are likely to have greater success, thereby promoting these novel mutualisms. In this stage, the abundance of the non-native drives mutualism formation and stability, in a neutral process. By contrast, in systems where non-natives established long ago and become integrated into the community, traits that enable their partners to maximize benefit from these relationships should be favored by natural selection and lead to niche-based adaptation. It is also possible that adaptation of native partners to a non-native species may result in cheating or a rise in extinction probability if associating with the non-native species results

in dependence on an unreliable partner, a process typical of an evolutionary dead-end (Schlaepfer et al. 2002).

The relative importance of neutral vs. niche processes may also be explored through mutualistic network models. For example, asymmetric specialization or nestedness is a pervasive feature of known mutualistic networks (Vázquez and Aizen 2004; Bascompte and Jordano 2014; but see Blüthgen 2010) in which the abundant, generalist species in one trophic group (e.g., plants) preferentially interact with many rare, specialist species in the other trophic group (e.g., pollinators) and vice versa. “Forbidden links” in mutualistic networks result from niche differences, when species do not overlap in space or time (e.g., a plant flowers and senesces before an insect emerges, *sensu* Bascompte and Jordano 2014). Non-native species, particularly after establishment, may be present across more seasons and in more locations than natives, reducing the occurrence of “forbidden links” in the community. For example, *Calotropis procera* flowers and fruits continuously in invaded Brazilian shrublands compared with a 2-6 month window in its native range, potentially bridging the phenological gap between native species that often flower in either the dry or wet season (Sousa Sobrinho et al. 2013). Similarly, the non-native tree *Ligustrum lucidum* presents food at a different season than its co-occurring native fleshy-fruited trees in Argentinian dry forests, providing frugivores with a fruit resource in an otherwise resource-poor season (Ferreras et al. 2008). Thus, non-native species that become abundant may serve as constant and abundant partners for native mutualists, bridging modules in mutualistic networks that are separated by space or time (Olesen et al. 2007). The inclusion of abundant non-natives into native mutualism networks does appear to shift the behavior or traits of native mutualists (Olesen et al. 2002; Aizen et al 2008; Kaiser-Bunbury et al 2011). Clearly, the relative importance of niche and neutral processes in mutualisms is a topic that requires greater investigation, and novel mutualisms present such an opportunity.

Tackling new questions and new systems with novel mutualism research

As our discussion illustrates, novel mutualisms may serve as prototypes for the study of mutualism formation and thresholds in mutualism strength and exploitation. Using novel mutualisms as model systems to better understand how species enter and establish in communities may help advance basic research and fill current understanding gaps. Because they are widespread and dynamic, novel mutualisms are promising focal points for a diversity of outstanding basic questions (Table 1), and such work may build on the strong foundation in novel mutualism research established by scientists working to understand the importance of positive interactions in a context of biological invasions (e.g., Richardson et al. 2000; Klironomos 2003; Ness 2003; Traveset and Richardson 2006; Aizen et al. 2008; Kaiser-Bunbury et al. 2011; Rodríguez-Echeverría et al. 2012). Our hope with this Commentary is to stimulate interest in novel mutualisms by researchers working across systems and subdisciplines. A deeper understanding of the role of novel mutualisms in marine systems is a particular need. The history of ecology as a discipline

Table 1. Examples of questions in ecology and evolutionary biology that could be addressed with novel mutualisms as focal systems.

Research questions	
<i>Basic ecology</i>	
•	Do novel mutualisms promote stability, resilience, and diversity in ecological communities, as native-native mutualisms appear to do?
•	Do mutualistic networks containing non-native species demonstrate the same architectural traits or level of stability as native networks?
•	Do novel mutualisms result from availability of open ecological niches?
•	Might specialization, at the level of the non-native or native interactors, dictate whether novel mutualisms can form?
•	When non-natives establish in interaction networks, to what degree and in what ways are they redundant with native participants?
•	Are some types of interaction networks more easily invaded?
•	Are invaded networks more or less resilient to future extinctions than non-invaded networks?
<i>Evolutionary biology</i>	
•	What can the formation of novel mutualisms—where coevolutionary history is lacking—tell us about mutualism evolution?
•	Do non-native mutualists impose or respond to the same selective pressures as native mutualists, and what are the evolutionary implications of novel mutualisms for native species?

has included examples of generalizable concepts developed in marine systems (e.g., keystone species, Paine 1969; trophic cascade research, Strong 1992). If a true dearth of novel ecosystems in marine systems exists, the development of theory surrounding their absence may help us to better understand fundamental differences among systems.

A diversity of modern research challenges may benefit from a better understanding of mutualism formation and stability and of the roles of functional traits and niche and neutral processes in emergent ecosystem properties. As one example, we can focus on microbial mutualisms, increasingly being recognized as critical players in a wide diversity of previously-unknown contexts (Redford et al. 2012; Sikes et al. 2012). Ecological research on gut and cutaneous microbial mutualisms in animals is still in its infancy, particularly compared to that of endophytic plant mutualists (McFall-Ngai 2008). Mutualisms with microorganisms include diffuse (e.g., lichens; O'Brien et al. 2005), generalist (e.g., some gut bacteria; Montalto et al. 2009), and specialized (e.g., endophytes; Arnold and Lutzoni 2007) partnerships. Most animal-microbial symbioses are thought to be obligate mutualisms (e.g., some *Wolbachia*-host relationships; Kozek and Rao 2007), but microbial invasions are likely rampant and may follow similar rules as invasions by macrobiota (Litchman 2010). Understanding these invasions is more than academic; novel microbial mutualisms may play an increasingly important role in conservation. For example, the emerging fungal pathogen *Batrachochytrium dendrobatidis* is causing global declines in amphibian populations, stimulating conservation research into the potential for inoculation of healthy amphibians with protective skin microbiota in order to reduce susceptibility to the pathogen

(Daskin and Alford 2012). Given the enormous diversity of microorganisms, research in this field holds much promise (McFall-Ngai 2008) and provides a potential proving ground for many of the predictions of this Commentary.

Conclusion

Biological invasions will continue to foment novel mutualisms in every system, with unforeseen consequences for native communities. These organisms provide unprecedented opportunity to observe the early stages of interaction development, and to directly observe processes that can be addressed only inferentially using traditional study systems and species. We suggest that novel mutualisms represent an excellent test arena for current understanding of mutualism formation, mutualism stability, functional traits, and niche vs. neutral processes. Novel mutualisms lend themselves to an expanded set of questions and research systems. Expansion and deepening of novel mutualism research can create synergy between invasion biology, basic ecology, and evolutionary biology, to the *mutual* benefit of all three.

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