Trends in Ecology & Evolution

Review

The Impact of Mutualisms on Species Richness

Guillaume Chomicki,[1,2,*] Marjorie Weber,[3] Alexandre Antonelli,[4,5,6] Jordi Bascompte,[7] and E. Toby Kiers[8]

Mutualisms – cooperative interactions among different species – are known to influence global biodiversity. Nevertheless, theoretical and empirical work has led to divergent hypotheses about how mutualisms modulate diversity. We ask here when and how mutualisms influence species richness. Our synthesis suggests that mutualisms can promote or restrict species richness depending on mutualist function, the level of partner dependence, and the specificity of the partnership. These characteristics, which themselves are influenced by environmental and geographic variables, regulate species richness at different scales by modulating speciation, extinction, and community coexistence. Understanding the relative impact of these mechanisms on species richness will require the integration of new phylogenetic comparative models as well as the manipulation and monitoring of experimental communities and their resulting interaction networks.

Mutualisms and Species Richness: An Ecological and Evolutionary Conundrum

Mutualisms – cooperative interactions among different species – are ubiquitous, have shaped much of global biodiversity, and have allowed organisms to access or outsource crucial functions such as transport, nutrition, cleaning, and defense. A large body of research has suggested strong links between mutualisms and the generation and maintenance of species diversity on Earth. However, this suite of hypotheses is complex, spans multiple scales, and can at times be contradictory. For example, at the ecological scale, May [1] argued that mutualisms have no effects on species diversity within communities. He argued that, because negative **density-dependence** (see Glossary) favors the coexistence of multiple species, mutualisms – which are associated with positive density-dependence – should do the opposite. This was later contrasted by newer empirical and theoretical studies highlighting asymmetry in the effects of mutualisms and suggesting that the formation of mutualistic networks plays a key role in promoting coexistence among multiple species [2–4]. The debate continues, with some researchers suggesting that species interactions including mutualisms play little role in shaping evolution [5], and that partnerships tend to stabilize species rather than promoting their diversification [6]. By contrast, a growing body of work claims the opposite, namely that mutualistic partnerships are an integral driver of morphological and evolutionary diversification [7–9].

In this review we ask when and how mutualisms influence diversity. Instead of including other metrics of diversity, we specifically focus on species richness to simplify our approach. Because this topic is so broad, we focus on two major areas of research. In the first we address how mutualisms impact lineage diversification rates, and in the second we examine how mutualisms impact on community coexistence, focusing on the modulation of competition dynamics.

Highlights

There are contrasting hypotheses about the influence of mutualisms on species richness.

We provide a synthetic framework for how mutualisms influence species richness at the ecological and evolutionary scales.

Mutualisms can promote or restrict species richness depending on their function, level of dependence, and specificity.

Because the outcomes of mutualisms are highly dependent on environmental variables, we forecast that the effects of mutualisms on species richness are also strongly influenced by biotic, abiotic, and geographic variables across ecological and evolutionary timescales.

Although our review depicts the complex and multifaceted impact of mutualisms on species richness, it also highlights a key gap: our understanding of the relative importance of the mechanisms through which mutualisms affect biodiversity. We suggest new methodological approaches to fill this gap.

[1] Department of Plant Sciences, University of Oxford, South Parks Road, Oxford OX1 3RB, UK
[2] The Queen's College, University of Oxford, High Street, Oxford OX1 4AW, UK
[3] Department of Plant Biology, Michigan State University, East Lansing, MI 48824, USA
[4] Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AE, UK
[5] Department of Biological and Environmental Sciences, University of

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Mutualisms Modulate the Regional Species Pool through Speciation and Extinction Dynamics

Five Ways through Which Mutualisms Drive Species Diversification

Mutualisms may promote diversification by either increasing the rate of speciation, decreasing the rate of extinction, or both (Figure 1 and Table 1). These effects could take place over whole clades, with mutualisms increasing the overall net diversification rate of a clade, thereby leading to mutualistic lineages with higher diversification rates than nonmutualist clades. Alternatively, mutualisms could affect diversification dynamics within a mutualistic clade, such as through the establishment of new partners or changes in the specificity or dependence of interactions. Here, we unpack five mechanisms by which mutualisms are hypothesized to impact on lineage diversification.

First, a key mechanism by which mutualisms can enhance speciation is through partner shifts. Partner shifts, especially when the new mutualistic partner differs in key functional traits, can drive **divergent selection** that can directly mediate speciation. This has been especially well established in plant–pollinator mutualisms, where acquiring a new partner differing in key traits affecting pollen transfer (e.g., bees vs birds or hawkmoths) leads to divergent selection in flower structure. In this case, the host shift then promotes speciation by interrupting gene flow [10,11]. Acquiring the new partner can directly impact on reproductive isolation via divergent selection, leading to increased rates of speciation. However, in pollination mutualisms, several mechanisms other than pollinator shift influence divergence (reviewed in [12]), implying the need to integrate ecological data into phylogenetic models of partner-shift speciation.

Second, acquiring a new mutualistic partner, either via a partner shift or *de novo* mutualism evolution, can also increase **ecological opportunity**, which can indirectly promote speciation. Ecological opportunity is thought to promote speciation by allowing a species to access previously inaccessible resources via enlarging its realized niche, with the potential to lead to adaptive radiation. Examples are found in primates: upon the evolution of frugivory, primates expanded their niche, and this fueled their diversification [9]. Similarly, mussel and sponge hosts exploit extreme marine environments owing to their ability to access energy from

Gothenburg, Gothenburg, Sweden
[6]Gothenburg Global Biodiversity Centre, Gothenburg, Sweden
[7]Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland
[8]Department of Ecological Science, Vrije Universiteit Amsterdam (VU University), De Boelelaan, 1081 HV, Amsterdam, The Netherlands

*Correspondence:
guillaume.chomicki@gmail.com (G. Chomicki).

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Figure 1. Mutualisms Affect Diversification. (A) The leaf beetle *Cassida rubiginosa* can only feed on leaves and degrade pectin because of its *Stammera* symbionts (inset) [17]. Such symbionts increase the ecological opportunities for the host, and the genus *Cassida* has radiated to >400 species. (B) Extrafloral nectaries (EFNs) increase plant survival when herbivore pressure is high, and species with EFNs have consistently higher diversification rates [8]. The ant here is *Odontomachus hastatus*, visiting an *Inga* EFN in Tambopata, Peru. (C) *Clermontia hawaiiensis* (Campanulaceae) is a plant endemic to Hawaii. Extinction of its honeycreeper pollinator led to population decline because the plant has a highly specialized corolla [44]. Photo credits: (A), Wikipedia (inset, Hassan Salem); (B), Aaron Pomerantz; (C), Karl Magnacca.

chemosymbionts (e.g., [13]), and gall-inducing midges form symbioses with fungi – wherein the midge creates a gall on a leaf, depositing fungal symbionts that feed and defend larvae – both of which expand niche space and fuel diversification [14]. Increases in ecological opportunity could also result from partner shifts, for instance in the case of plants shifting to a new pollinator group [15]. However, it is not always clear whether it is the mutualism itself that drives diversification via ecological opportunity. Confounding factors, including shifts in morphological traits and life history, are often correlated with mutualism evolution. For instance, predatory clownfish that form mutualistic partnerships with anemones that provide defense have higher diversification than their nonmutualistic relatives, but it is unclear whether the apparent ecological radiation is due to confounded life-history traits of the clownfish – including species-specific communication which reinforces reproductive isolation – or to the mutualism with sea anemones itself [16]. These confounding factors call for the development of new phylogenetic tools wherein multiple factors can be accounted for (Box 1).

Insect–microbe symbioses provide some of the most dramatic examples of increased diversification. Well-documented cases include herbivorous insects feeding on complex, recalcitrant plant material with the aid of pectin-degrading symbionts [17], and mealybugs surviving on a nutrient-limited diet supplemented by partnerships with nutrient-provisioning bacterial endosymbionts [18]. This positive effect of mutualistic symbioses on diversification is illustrated by several independent radiations of sap-sucking insects, totaling tens of thousands of species, which can only obtain nutrients from their hosts through their obligate endosymbionts [19,20].

Third, although radiations are likely driven by partner shifts, another important mechanism is probably host–symbiont incompatibility, namely a deleterious or selfish symbiont mutation that is not compensated by a host mutation, leading to hosts that cannot survive with a particular symbiont. In some insect–bacteria endosymbioses, host–symbiont incompatibility evolves because of deleterious allele fixation in bacterial symbionts that become fixed owing to clonality and small effective population sizes, as well as to within-host selection [18]. Insect hosts respond by compensating for these mutations, which in turn drives lineage-specific incompatibility, potentially accelerating speciation [20]. This mechanism is analogous to antagonistic arms-race coevolution where host and antagonists adapt and counter-adapt to one another.

Fourth, mutualisms can promote diversification by increasing range sizes, thereby decreasing extinction rates. Range sizes are strong predictors of extinction risk [21]. This is illustrated in numerous biotic seed-dispersal mutualisms, where proficient dispersers promote larger geographic ranges, potentially decreasing extinction and increasing the probability of speciation. For example, the repeated evolution of ant-dispersed plant clades led to more speciose lineages [22]. Similarly, in the plant order Fagales, which includes oaks and chestnuts, the evolution of biotic dispersal is associated with larger range sizes and higher diversification rates compared with species with abiotic dispersal [23].

Fifth, an additional mechanism leading to species diversification involves mutualisms that can decrease extinction risk by increasing the survival of individuals, for example in the face of high antagonist pressure or abiotic stress. For instance, defense mutualisms protect their partners against antagonists and thus decrease mortality associated with consumption or damage. One example is the formation of extrafloral nectaries (EFNs) in plants, nectar glands outside the flowers that promote arthropod defense. These glands attract predacious ants, which actively deter herbivores. Plants with EFNs have evolved hundreds of times independently and are associated with increased diversification rates relative to their non-EFN-bearing close relatives

Glossary

Cospeciation: concurrent speciation events in interacting lineages. Typically, cospeciation requires one-to-one partner specificity and parent to offspring (vertical) transmission.

Density-dependence: dependence of population growth of a species on the abundance (density) or another species. Density-dependence can be negative if the abundance of a species inhibits the population growth of another species, or positive, if it facilitates it.

Divergent selection: selection that drives the accumulation of changes in distinct populations of a species, typically leading to speciation.

Diversity-dependence: dependence of the diversification rate of a lineage on the species richness of another lineage, interacting directly or indirectly. For example, competing lineages are thought to exhibit negative diversity-dependence on each other.

Ecological opportunity: the wealth of evolutionary accessible resources that are available to a particular lineage.

Equalizing effects: a species coexistence mechanism which acts by reducing fitness differences among species.

Geographic mosaic of coevolution: the integration of the spatial dimension of coevolution (reciprocal trait change between interacting taxa driven by natural selection), highlighting that coevolution is uneven across the geographic landscape, with hotspots of tight coevolution and ‘coldspots’ where selection operates only on one species or on neither species.

Higher-order network: a group of network approaches that take into consideration more dynamic data to represent networks than do conventional approaches, for instance by differently stratifying the network according to different time-layers where the interactions were recorded.

Host sanction: a mechanism by which a host can punish less-effective symbionts. The concept does not account for evolutionary origin (i.e., host sanctions can derive from ecological fitting or/and selection from cheating).

[8]. However, a link between increased individual survival and altered extinction or speciation rates has not been empirically documented in this system, and deserves further attention more generally. Experimental evolutionary approaches in short-cycling species can help to fill the gap between individual survival and speciation and extinction. Promising systems include mussel–cordgrass mutualism in salt marshes [24] – where mussels transfer nitrogen to the marsh sediments, stimulating cordgrass growth, in return for an environment with reduced heat and predator stress for the mussels – or the grass–fungal endophyte symbioses [25], where fungal endophytes provide protection to the host grass against abiotic and biotic stresses. Using systems such as these, we can begin to ask specific questions about how increased survival and resistance to abiotic stress (e.g., drought) drives changes in diversification rates.

Finally, one often-cited mechanism linking mutualism to diversification dynamics is **cospeciation** (reviewed in [26]). However, although cospeciation matches the timing of speciation events in host and symbiont lineages, there is no strong evidence so far that it affects diversification rates *per se*. Thus, we do not consider it as a potential mechanism through which mutualisms influence species richness at the geological scale.

Four Mechanisms by Which Mutualisms Can Slow Down Species Diversification

We have so far argued that mutualisms can enhance diversification directly [via (i) partner shifts or (ii) host–symbiont genetic incompatibility] or indirectly [via (iii) increasing ecological opportunity, or decreasing extinction by (iv) enlarging range size or (v) enhancing individual survival; Table 1]. However, mutualisms are also hypothesized to have the opposite effect, reducing lineage diversification rates, thereby decreasing the richness of the regional species pool. We identify below four mechanisms by which mutualisms are hypothesized to decrease lineage diversification rates, thus reducing clade species richness.

First, mutualistic partnerships may restrict diversification via ‘stabilizing coevolution’ processes. Theory suggests that partners can exert stabilizing selection on various traits involved in mutualisms [6,27–29]. In highly specialized and dependent mutualisms, where a species depends on a single or very few partner species, there is the potential for greater trait matching. Trait matching, such as the shape of a flower corolla perfectly fitting the shape of a bird’s beak, can limit speciation because the match increases partner fitness [6]. Although trait matching has been shown to reduce the pace of morphological evolution in both pollination [30] and epiphytic ant–plant [31] mutualisms, more empirical data will be necessary to link trait matching to decreased diversification rates. New classes of diversification models that explicitly account for interacting partners and mutualistic traits (Box 1) can help to verify theoretical predictions. Although the link between diversification and ‘stabilizing coevolution’ is an exciting area, more research is needed.

Second, in many specialized symbioses, hosts restrict symbiont genetic diversity, and this could lead to decreased rates of lineage diversification. For example, when hosts control the reproductive fate of their symbionts, this can drive the degradation of genetic diversity in the symbionts. Although such a reduction in symbiont diversity can decrease conflict among competing symbiont lineages [32], it can also impose vulnerabilities. For example, in endosymbioses that are transmitted vertically from parents to offspring, extensive symbiont genome decay has led to some of the smallest known genomes to date [17,20,33]. Although symbiotic replacement processes can rescue hosts from degrading partners, there is a substantial risk of hosts becoming trapped in a ‘rabbit hole’ whereby irreversible codependence entails higher risks, including the accumulation of deleterious mutations, reduced environmental tolerance, and so forth [20]. This has been well documented in insect–microbe

Island biogeography theory: the seminal conceptual framework published in 1967 by Robert MacArthur and Edward O. Wilson that provided the foundation for island biogeography and in particular provided a series of predictions linked to area–diversity patterns, colonization, and dispersion.

Lottery model: a competition model wherein randomness plays an important part in success, for instance where many seedlings compete for a tree gap, and one is randomly ‘chosen’ to be recruited. It also relates to the priority effects, wherein the time of arrival has an important consequence for competition, and randomness across species can thus promote coexistence.

Mutualistic networks: a representation of the community-wide interactions between plants and their animal mutualists that result from the application of network theory. These bipartite networks are based on observations of real communities and can be analyzed in terms of their topological properties.

Nestedness: a pattern identified in mutualistic networks wherein specialized mutualists interact with the most generalist mutualists.

Stabilizing effects: a species coexistence mechanism that tends to increase intraspecific versus interspecific competition by making species more different from one another. Stabilizing mechanisms are viewed as being more important in promoting stable species coexistence.

Storage effect: a mechanism that stabilizes species coexistence and implies that, in a changing environment (spatially or temporally), not all species can be best in all conditions, which affects recruitment probabilities – with some species doing well in some locations but not in others, thus promoting species coexistence.

Taxon cycle: a hypothesis for biogeographic dynamics in space and time where particular traits and ecological attributes favor range expansion, but that such large ranges are unstable, ultimately leading to the evolution of species fragments that are specialized to particular habitats.

Table 1. Mechanisms through Which Mutualisms Can Impact on Species Richness

Effect on species richness	Scale	Mode of action	Direct or indirect	Description of the mechanism	Type of evidence[a]
Positive	Macroevolutionary	Speciation	Direct	Partner shift promotes divergent selection and interrupts gene flow	D, P
Positive	Macroevolutionary	Speciation	Indirect	Ecological opportunity: niche broadening	D, P
Positive	Macroevolutionary	Speciation	Direct	Host–symbiont incompatibility	P
Positive	Macroevolutionary	Extinction	Indirect	Decreasing extinction by increasing range size	D, P
Positive	Macroevolutionary	Extinction	Direct	Decreasing extinction by increasing survival	D, P
Negative	Macroevolutionary	Speciation	Direct	'Stabilizing coevolution' limits trait variation via stabilizing selection	P, T
Negative	Macroevolutionary	Speciation	Direct	Host restricts symbiont genetic diversity	P
Negative	Macroevolutionary	Extinction	Indirect	Extinction via ecological niche restriction	P
Negative	Macroevolutionary	Extinction	Direct	High mutualistic dependence can lead to coextinction cascades	P
Positive	Community	Stabilizing effect	Direct	Negative density-dependence driven by asymmetry	E
Positive	Community	Stabilizing effect	Direct	Niche differentiation driven by mutualism in space, time, or along ontogeny	P, E
Positive	Community	Stabilizing effect	Direct	Priority effects randomize the success of alternative mutualists	P, E
Positive	Community	Stabilizing effect	Direct	Storage effects support a diversity of mutualists in a changing environment	P, E
Positive	Community	Equalizing effect	Direct	Natural genetic variation in the ability to sanction uncooperative partners	P, E, T
Positive	Community	Equalizing effect	Direct	Partner mismatch: mutualists can be very effective on some partners but ineffective on others	P, E
Positive	Community	Equalizing effect	Direct	Context-dependence supports a diversity of mutualists across a heterogeneous landscape	P, E, T
Negative	Community	‘Destabilizing’ effect	Direct	Positive density-dependence, favoring a specialized partner, which can become competitively superior within a community	P, E, T
Negative	Community	‘De-equalizing’ mechanism	Direct	Population structure in one partner (typically symbionts) reduces the variation available to the hosts	P, T

[a] For the types of evidence, D refers to lineage diversification rate analyses based on molecular phylogenies, P refers to an observed pattern or observation that is consistent with the mechanism proposed, E to experimental demonstration, and T theoretical prediction.

symbioses [17,20,33]. The widespread asymmetry in species richness between host-rich and symbiont-poor lineages suggests that host control of symbiont genetic diversity is an important mechanism by which symbiotic mutualisms influence species richness. Testing this hypothesis will require large-scale phylogenetic studies of symbiotic lineages and their nonsymbiotic relatives.

Box 1. Developing New Phylogenetic Tools to Test for Patterns Consistent with a Role for Mutualisms in Diversity Dynamics

Evaluating hypotheses about the mechanisms by which mutualisms drive lineage diversification (see Table 1 in main text) will require the implementation of new phylogenetic tools that extend beyond state speciation and extinction models (e.g., [70]). In particular, there is a need for methods that explicitly account for multiple interacting clades, modeling partner shifts, diversification rate shifts, biotic traits (see below), and abiotic factors.

Recent developments in trait matching and coevolutionary models [71–73] are expanding our ability to analyze complex evolutionary patterns. However, extending these models to account for multiple interacting clades and lineage diversification rates is an exciting opportunity for development. Incorporating lineage diversification requires that the degree of trait matching negatively influences the probability of speciation. As in Drury *et al.* [72], trait matching should be parameterized to possible only if interacting species are sympatric by explicitly incorporating a spatial component in the model.

Because species interactions are context-dependent in ecological and evolutionary time, future phylogenetic models incorporating mutualisms will also need to account for variation in other factors that are known to impact on the mechanisms discussed above. For example, incorporating environmental and/or trait variation will greatly enhance the biological realism and utility of the models. Temporal variation in abiotic factors [74], as well as fluctuations of abiotic variables such as temperature and precipitation, could be modeled as directly modulating the effect of mutualism on diversification. This would allow us to test major hypotheses in mutualism evolution, such as the expectation that highly specialized mutualisms put species at higher risk of extinction [42,43].

An additional development would be to extend phylogenetic diversity-dependent models to include positive diversity-dependence, as is found in some mutualisms. This would allow tests of hypotheses such as whether the diversity of pollinators positively influences the speciation of its plants, for instance by increasing the probability of partner shifts [75].

Because molecular phylogenies alone offer limited insights into extinction, there is great scope to focus on groups with an extensive and informative fossil record. The marine realm offers several options [76]. Another approach is to use the fossil record directly, such as under the probabilistic Bayesian framework implemented in the software PyRate ([77]; for empirical examples applied to species interactions and methodology applicable to mutualisms refer to [78,79]). Ultimately, an expanded phylogenetic comparative modeling toolkit will enhance our ability to test for patterns consistent with mutualism-driven diversification dynamics.

Cases of host restriction of symbiont genetic diversity also occur in agricultural mutualisms. In ant–plant farming symbioses, ant farmers cultivate sibling plants together, generating plant social structure that likely reduces outbreeding [34]. In fungus-farming termites, termites directly promote low diversity of the fungal symbiont because fungal monocultures are key to stabilizing cooperation despite horizontal (environmental) symbiont transmission [35]. The ultimate level of host control is when symbiont reproduction is so tightly linked to host reproduction that it becomes an organelle-like structure [36]. The frequency with which hosts decrease symbiont diversification in this way is an open field of research, and comparative phylogenetic approaches will be necessary to statistically test for this effect across interacting clades.

Third, mutualisms can also decrease diversification rates by increasing extinction risk, which can take place in at least two different but often complementary, ways. For one, mutualisms can increase extinction risk by decreasing the realized niche of a species, for example if one partner has a narrower fundamental niche breath than the other. In insect–microbe endosymbionts, mutations and losses of nutritional genes in both endosymbionts and hosts can restrict insects to specific food plants [37–40], reducing niche breadth in ways that could increase extinction risk. In another example, endosymbiontic *Blochmannia* bacteria have a higher temperature sensitivity than their carpenter ant (*Camponotus*) hosts [41], potentially limiting the range size of their host.

Fourth, high extinction risk may exist when partner loss has high fitness costs, such as in obligate and specialized mutualisms. This may be especially important when the specialized partners are acquired anew each generation via horizontal transmission, and thus risk being lost, for instance owing to lack of partner availability during early developmental phases [42]. Extreme specialization and dependency can also increase extinction risk by binding partners into a coextinction cascade [43]. This can happen when one partner becomes extinct or undergoes substantial population decline. One example involves several bird-pollinated plant species endemic to the Hawaiian islands in the plant family Campanulaceae, which are now threatened as a consequence of the human-driven extinction of Hawaiian honeycreepers. In this case, non-native pollinators cannot rescue the mutualist because of the specialization of flower morphology [44]. Similarly, in the same way as host–symbiont genetic incompatibilities can drive speciation by forcing host compensation and creating lineage-specific incompatibilities, such incompatibilities may also increase extinction risk because specialization prevents outside options [20]. Finally, recent phylogenetic comparative analyses suggest that specialized and obligate mutualisms are often evolutionarily irreversible dead-ends because no transition backwards can be inferred, whereas generalist and facultative mutualisms are often evolutionary labile, as inferred by frequent evolutionary transitions back and forth [31,46]. These studies further support the idea of increased extinction threats in obligate mutualisms.

Although a growing body of evidence links mutualisms to species richness via speciation and extinction dynamics, more work will be necessary to connect larger macroevolutionary patterns with ecological processes such as mutualistic function, level of partner dependence, and partner specificity. Work that develops mutualism-based phylogenetic comparative methods (Box 1) and integrates these models with microevolutionary (e.g., population and quantitative genetic) studies and experimental manipulations (Box 2) will be particularly fruitful for linking

Box 2. Interaction Networks and Community Manipulations to Decipher the Role of Mutualisms in Species Coexistence

Species coexistence within a community cannot be considered as only a sum of pairwise interactions [80]. Analysis of the structure of mutualistic networks has led to major insights into the role of mutualisms in promoting community coexistence. A key finding of such analyses is that mutualistic networks often have a nested architecture, meaning that specialist species interact with subsets of generalist species [2]. Specialists tend to interact with generalists that show less fluctuation in time and space, thus increasing network robustness and coexistence [2,81]. Such **nestedness** has been predicted to enhance the number of coexisting species by reducing effective interspecific competition [4]. Moreover, it has been argued that, once mutualistic networks reach a minimum complexity, this allows other species to ‘attach’ to the network, increasing network size [82], suggesting that network size positively feedbacks on species coexistence.

The above effect of the structure of mutualistic networks on species diversity can be understood as the balance between network contributions to both fitness and niche differences [83]. This study helps to relate the body of work on mutualistic networks with empirical studies on species coexistence in competitive systems. It also suggests the need to characterize the structure of competition within communities [80], which is often assumed to be similar across species but may affect how mutualistic networks impact on biodiversity [84]. A recent study using different tropical islands where animal dispersers were excluded revealed that seedling species richness was twice as large in the presence of animal dispersers [85]. This echoes earlier work in Peruvian rainforests, showing that when large vertebrate dispersers are depleted, tree sapling recruitment and species richness decline [86].

To test the hypothesized effects (see Table 1 in main text) of mutualism on species coexistence and their relative importance in species ecological dynamics, we propose the integration of network-based approaches at multiple scales. A promising approach is to manipulate experimental communities by adding and removing mutualists. Ideally, experimental communities could be manipulated and species abundances, richness, and interactions monitored. The key would be to (i) record all interactions, not only mutualistic, and (ii) use a network approach to analyze the experimental results in addition to other parameters. These data could address the effects of mutualism as modulators of species coexistence and explicitly quantify species niche differences (stabilizing) or fitness differences (equalizing) effects. This approach could also incorporate abiotic environmental variables such as light level, temperature, and precipitation. Manipulations of experimental communities across generations in fast-generation species could allow researchers to bridge ecological and evolutionary scales. In this regard, microbial communities could be a useful resource.

species richness with the many mechanisms by which mutualisms could impact on speciation and extinction. The development of 'model clades', wherein solid phylogenetic data are available, concurrent with abundant ecological data for all species of the clade, can help to test the generality of mechanisms and make links between ecological processes and diversification patterns.

Mutualisms Affect Species Coexistence by Modulating the Effects of Competition

Ecological theory has long emphasized the role of some antagonistic interactions – notably competition – in promoting species richness within communities via coexistence (reviewed in [47]). Although this perspective started to shift two decades ago, the relative importance of mutualisms in promoting species coexistence within different communities remains poorly known. We identify below several mechanisms through which mutualisms can promote or restrict species coexistence via stabilizing and equalizing effects, and discuss the relative importance of mutualism in shaping species coexistence within communities (Box 2).

Stabilizing Effects of Mutualisms Can Promote Stable Species Coexistence by Altering the Outcomes of Competition

Negative feedback on species abundances, known as negative **density-dependence**, is thought to be the primary driver of species richness within communities, and is generally attributed to competition, predation, and parasitism [46]. In a seminal paper, May [1] proposed that, because mutualisms do not generate negative feedback in species abundances, they do not contribute to species coexistence. It is now recognized that this view is limited. We describe below four ways through which mutualisms contribute to coexistence via stabilizing mechanisms – either by increasing negative intraspecific interactions or by decreasing negative interspecific interactions.

First, asymmetry in mutualisms can increase negative intraspecific density dependence, thereby promoting coexistence. Asymmetry in the delivery of benefits can lead to mismatches between mutualists, such that the preferred partner of a mutualist does not provide the highest benefit compared with alternative partners. Such asymmetry, in turn, can directly drive negative feedback on abundances of the mutualist, and hence promote species coexistence, contradicting May's assumption. A textbook case occurs for mycorrhizal symbiosis wherein the fungus that grows best with a particular plant host is a poor nutritional partner for the host plant [48]. More generally, the asymmetry of control in mutualistic interactions often generates negative density-dependence (e.g., [48]). This feature expands to another level of complexity: **mutualistic networks** where asymmetry in species dependencies is rampant and is thought to be essential for the robustness of the system (Box 2), and may also promote negative density-dependence.

A second important stabilizing mechanism by which mutualisms can promote species coexistence is by increasing niche differentiation and partitioning, thereby decreasing negative interspecific interactions. Both processes can occur in space, time, or along ontogeny. One example is the divergent selection operating on arbuscular mycorrhizal fungal genes which are linked to their evolutionary history on different soil types. A well-studied case revealed niche differentiation leading to a fungus-driven habitat preference in two sympatric palm species [50]. Niche differentiation driving coexistence can also arise as a result of nonlinear competitive feedbacks between symbiont-bearing and symbiont-free hosts, as in the grass–endophyte symbiosis [51]. An example of mutualisms partitioning niches in time would be, for instance, a plant associating with a range of pollinators with differing foraging times [52], including diurnal and nocturnal pollinators [53]. Niche partitioning along ontogeny is found, for example, in African ant–acacia symbiosis, where acacias favor successional changes in the four main ant symbionts, depending on the growth stage of the acacia. This prevents the competitive exclusion of the dominant ant partner within an acacia community [54]. This ontogenetic niche partitioning is also thought to occur in the development of coral reefs and their associated algal endosymbionts [55]. Similarly, an emerging theme in symbiotic research is within-host symbiotic coexistence. Although it has long been predicted to harm hosts [32], new research identified that multiple symbionts can coexist within a single host if they provide different functions [45].

A third mechanism of mutualism-facilitated stabilization is competition–colonization trade-offs among two or more potential partners, which can decrease interspecific negative interactions. In this case, the competitively superior partner is the poorer colonizer, which allows species coexistence across heterogeneous environments [56,57]. An example of this mechanism occurs in a Neotropical ant–plant symbiotic mutualism. In this case, two alternative ant partners coexist owing to a dispersal–fecundity tradeoff which favors the ant with higher dispersal ability in areas of low plant host density and the poorer-dispersing (but more fecund) partner in high-density areas, thus directly driving coexistence [58].

Finally, a fourth mechanism that stabilizes coexistence involves the order of arrival of mutualists within a particular community, the so-called priority effect. The idea is that the order of arrival determines the competitive hierarchy, and such order depends on randomness (**lottery model**) linked to dispersal. A recent study experimentally showed that the competitive ability of arbuscular mycorrhizal fungi (AMF) is time-dependent: well-established AMF can suppress invading AMF [59]. Similarly, endosymbiontic gut communities of bees show strong priority effects, and such functional differentiation may have important fitness consequences for the hosts [60]. A related mechanism, known as the **storage effect**, implies that, in a changing environment (spatially or temporally), not all species are equally good across all conditions. This, in turn, affects recruitment probabilities. Evidence for storage-effect coexistence can be found in ectomycorrhizal (ECM) symbioses, where fluctuating local conditions can shift recruitment times of different ECM fungi [61]. Although these classic coexistence mechanisms function within mutualistic systems, their weight in promoting community coexistence remains to be determined.

Equalizing Effects of Mutualisms Enhance Species Coexistence by Promoting Variability

Equalizing effects – *sensu* Chesson [47] – are mechanisms that lead species to be more equal in their competitive abilities. Although they are less well understood than **stabilizing effects**, they could also be an important mechanism by which mutualisms impact on species coexistence and thus on species richness in communities. We discuss three mechanisms by which mutualisms promote coexistence via equalizing effects.

First, equalizing effects among hosts could drive a differential ability to discriminate among competing symbiotic partners. A well-studied case occurs in legume–rhizobia mutualism, where natural genetic variation in the ability of the host plant to sanction ineffective rhizobia (**host sanction**) is thought to help to maintain the presence of poor partners in the symbiont pool [62]. Studies on plant–mycorrhizal symbiosis have reached similar conclusions [63], finding that hosts differing in their ability to discriminate among effective and ineffective fungal partners can maintain a larger pool of symbionts [64]. Why plants do not discriminate equally well is an open question.

Box 3. Mutualisms Influence Species Biogeography

Biogeography links ecology and evolution: species richness in a geographically confined system depends on speciation, extinction, and immigration. Mutualism influences these processes in several ways, and the study of biogeography can help to link mutualism to patterns of species richness.

First, mutualisms can influence range size, mediated in part by their degree of specialization and dependence. For example, species that depend obligately on one or few specific partners are restricted by the occurrences of their partner, as documented in ant–plant symbioses [87] and legume–rhizobia symbioses [88]. However, global tests of this idea are still lacking, but biogeographical approaches and large-scale datasets on mutualism specialization (and dependence) will allow this question to be addressed.

Second, considering mutualisms within the **taxon cycle** concept (reviewed in [89]) may alter some phases of the cycle. For instance, generalist mutualists should be much more likely to embark on the colonization of islands (expansion phase), as well as on range expansion and niche broadening (ecological release phase).

Third, mutualisms may affect the key predictions of MacArthur and Wilson's [90] **island biogeography theory**, which determine the relation between immigration, extinction rates, and species richness as a function of island size and distance from the continent. As pointed out by Bruno *et al.* [91], mutualisms, or facilitation more generally, can invert the relationship between successful immigration and species richness if the native species cooperate with the immigrant instead of competing. The same expectation holds for extinction rates. Mutualistic specialization should modulate the island area effect, with the more generalist species being less vulnerable to diversity-dependent extinction (because they can cooperate with more species).

The above considerations build on the traditional approach of biogeography. In the past few years, however, several attempts have been made to extend biogeography to species interaction networks. One conclusion of these studies is that if preserving species interactions – rather than merely species – were to be the target, one would need to preserve an up to fivefold larger area [92]. Further, a biogeographical approach to mutualism may allow quantification of partner fidelity by decomposing turnover on species co-occurrence from turnover on interaction given that the two partners co-occur [93,94].

An important step in further investigating the influence of mutualisms on spatial patterns of diversity would be to integrate species networks into so-called bioregionalization analyses. This will require the computation of species relationships over space (Figure I), and the use of **higher-order network** approaches (e.g., [95]) using information theory as previously applied for bipartite, single-species networks [96,97]. The spatially explicit networks would facilitate the prediction of new interactions of invasive species, especially when modeling true and false species absences under a Bayesian framework (e.g., [98]).

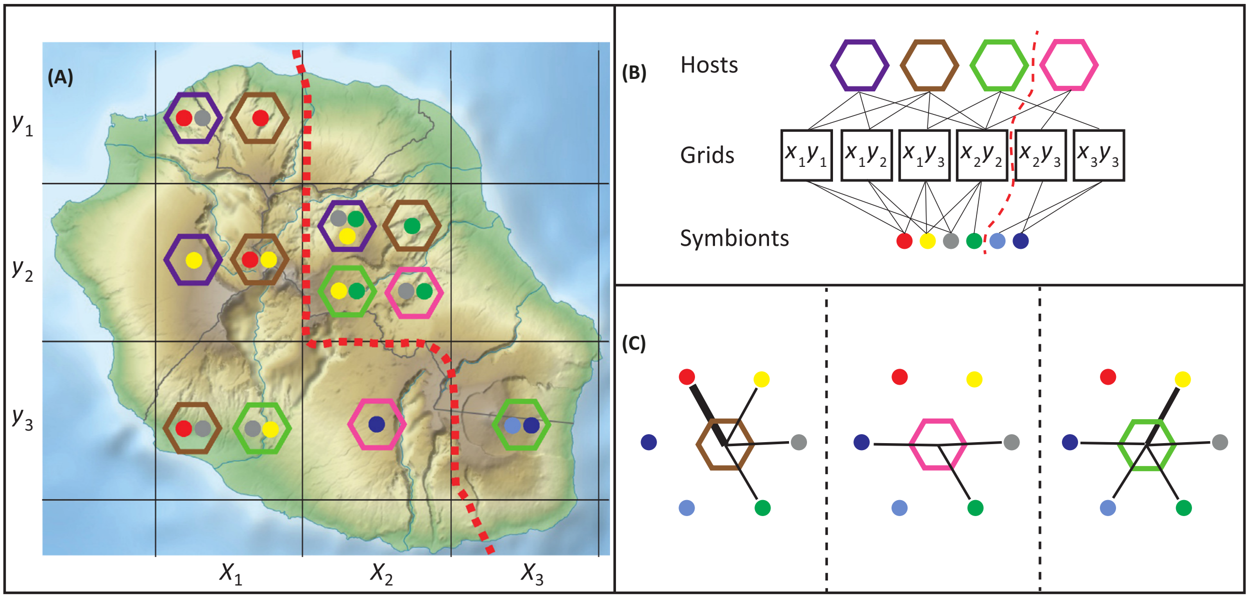

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Figure I. Spatial Visualization and Bioregionalization of Mutualistic Interactions. (A) The presence of host species (hexagons) and their symbiotic taxa (filled circles) is depicted in each grid cell. (B) Higher-level networks are created that contain the links (documented or predicted occurrence) of each host and each symbiont per cell. In (A) and (B) the red dashed line represents a natural break that separates two major clusters (bioregions), calculated using information theory. (C) A visualization of how many (number of connecting lines) and how often (line thickness, proportional to the frequency of occurrence in grids) hosts interact with the total available pool of symbionts. Such analyses can facilitate the identification of areas with high overall biological diversity, those particularly susceptible to the introduction of invasive species with specific interactions, and areas where particular symbionts can be expected to occur but have not yet been documented.

A second mechanism that could promote species coexistence by equalizing partner fitness is partner mismatch. Under the partner-mismatch hypothesis, some symbionts are ineffective on one host but beneficial on others [62]. This mechanism has been shown to also operate in legume–rhizobia symbioses, whereby the same rhizobial partner can have profoundly different fitness consequences for related host plant species [65].

Thirdly, similarly to partner mismatch, context-dependency can promote species coexistence by locally altering competitive hierarchies across different environmental contexts. This mechanism is especially relevant in mutualisms that span environmental gradients [66] because both the sign and the strength of the mutualistic interaction can change as a function of biotic and abiotic variables (e.g., light, nutrient, abundance of a particular species). As a result, an ideal partner in one condition may be a poor partner in another, leading to species coexistence as environmental conditions change through space or time [67].

Other Mechanisms by Which Mutualisms Restrict Species Coexistence

We have discussed how mutualisms can drive species coexistence by creating negative feedbacks on partner abundance, but some mutualisms do indeed create positive feedbacks, as May [1] predicted. Although those feedbacks can, in theory, support rare species and thus stabilize diversity, they can also promote dominant species and thus negatively impact on species coexistence. A good example is the mutualism between the common Amazonian tree *Duroia hirsuta* and *Myrmelachista schumanni* ants, which kill all vegetation other than their host plants in so-called devil's gardens. An 18 year study revealed that ants significantly increase the growth and survival of this common tree [68], thus negatively affecting species coexistence. This acts as a 'destabilizing' mechanism by making the mutualist competitively superior.

A second potential mechanism through which mutualisms could restrict species coexistence is by limiting dispersal and increasing relatedness in clustered populations of mutualists. In many symbiotic mutualisms, population structure arises especially in symbionts owing to the limitation of sexual reproduction. Population structure thus has the potential to directly limit partner diversity [69].

Clearly, both stabilizing and equalizing mechanisms link mutualisms to species coexistence at the community scale. However, more work will be necessary to elucidate the relative importance and ubiquity of these processes. This can be done in both laboratory and field systems, but a key criterion is that ecological manipulations and monitoring should be possible (Box 2). This can allow us to reach the goal of better integrating mutualism into modern ecological coexistence theory.

Concluding Remarks

We have outlined a suite of mechanisms by which mutualisms modulate species richness at ecological and evolutionary scales – both positively and negatively (Table 1). Our review reconciles seemingly contradictory hypotheses about the relationship between mutualism and the generation of biodiversity. There is now overwhelming evidence that mutualisms play an important role in modulating species richness across space and time. Nevertheless, the relationship is complex, and likely involves strong positive and negative feedbacks with the environment, notably with geography (Box 3) and abiotic variables (Box 4). Thus, one promising avenue for future research will be to further understand how the interaction between mutualisms and environmental variables drives species richness. Conducting research on mutualism along diversity and elevational gradients will be particularly useful in this regard. Moreover, several of the plausible mechanisms we propose are only supported by observational evidence

Outstanding Questions

What are the relative contributions of the different mechanisms identified (Table 1) in mediating the relationship between mutualism and species richness? Our review has identified a series of putative mechanisms by which mutualisms could influence species richness at the ecological and evolutionary scales. However, the relative importance of these mechanisms remains elusive, and this is a key knowledge gap that needs to be addressed.

How can we determine the overall contribution of mutualisms at a macroevolutionary scale given that they evolved in a nested manner in which the emergence of some mutualisms led to key innovations, and within which other mutualisms later arose and impacted on diversification? An example is the origin of mycorrhizal mutualisms, which dates back to the conquest of the land by plants, key fossils being found in the Rhynie chert of Scotland (407 Ma). Mycorrhizal symbiosis was a prerequisite, for instance, for the evolution of root endosymbioses with bacteria such as in legume–rhizobia symbiosis. How can we evaluate the impact on diversity of mutualisms with a nested origin?

What is the impact of different mutualistic interactions on coexistence of the same species? Mycorrhiza, for instance, positively influence pollination. However, other mutualistic interactions could annihilate each other, for example if a plant simultaneously attracts pollinators and ant-defenders. Because the majority of species are involved in multiple mutualisms, this could have consequences in terms of coexistence. For instance, additive positive effects could give some species higher competitive ability, thereby potentially decreasing coexistence within communities, but negative effects could either – at least in theory – promote coexistence further or reduce the coexistence-promoting effects of the respective mutualisms.

Are mutualisms more specialized in the tropics, and is this driving coexistence via niche partitioning? This long-held assumption remains unvalidated. However, the largest analysis to date

Box 4. Abiotic Mediation of the Relationship between Mutualisms and Species Richness

Because species interactions, including some mutualisms, are more prevalent in the tropics than in other zones, it has been hypothesized that such interactions play an active role in generating the latitudinal diversity gradient on land and in the sea [99,100]. Indeed, several mutualisms are restricted to low latitudes, such as ant–plant or coral–zooxanthelae symbioses ([100] for an exhaustive list). This raises the question as to what extent the intricate relationship between mutualism and species richness is mediated by abiotic factors. Some climatic factors, such as stable high temperature and precipitation, are simply more suitable for many species-forming mutualisms. The abiotic limitations for mutualism establishment have three major implications.

First, at the local scale, environmental variation will lead to a mosaic of interactions that favor different partners in distinct local environments. Such context-dependence directly promotes species coexistence (see Table 1 in main text). Thus, more variable environments (within which the mutualism can establish) will maximize the coexistence effect of context-dependency. Abiotic mediation of the abundance of a mutualist has been clearly shown in an ant–aphid mutualism [101]. In this case, aphid abundance varies with the light environment because tending ants are more abundant in full sunlight [101].

Second, the effect of mutualism on species coexistence across a heterogeneous landscape will lead to ‘hotspots’ and ‘coldspots’ of mutualism-driven coexistence. This idea is analogous to the **geographic mosaic of coevolution**, but is applied to the effect of mutualism on coexistence rather than intrinsic species traits. Along an environmental gradient, mutualism could thus promote a gradient of species coexistence. Thus, the interaction between mutualism and abiotic factors could enhance diversity gradients.

Third, abiotic limitation of mutualisms could also feedback on biodiversity in time. Do periods of extreme unstable climatic conditions differentially affect mutualistic versus nonmutualistic lineages? Strong support for this hypothesis is found among scleractinian corals, where the extinction rate of symbiotic corals was nearly fourfold higher than in asymbiotic corals at the Cretaceous–Tertiary mass extinction [102].

Thus, the mechanisms identified through which mutualisms could influence species richness at the evolutionary or ecological scale (see Table 1 in main text) operate only where environmental conditions are suitable for the mutualism to function fully. Because such conditions vary through time (e.g., climatic cycles of the Earth) and space (e.g., latitude), the impact of mutualisms on species richness is likely modulated by abiotic factors. This highlights how the context-dependence of mutualisms can link their effects on species richness across ecological and evolutionary scales.

or mere correlation. Future work should aim to formally quantify these links between mutualism and species richness. Furthermore, many outstanding issues remain, notably regarding quantitative evaluation of the extent to which each of the identified mechanisms affects species richness (see Outstanding Questions). This will require new innovative and integrative approaches, the generation of standardized and geo-referenced data on mutualistic interactions, and the development of new comparative phylogenetic tools (Box 1) and experimental approaches (Box 2). Ultimately, an integrated approach will bring us closer to fully appreciating the role of mutualism in shaping biodiversity on Earth.

has shown that, at least in some mutualisms, specialization is higher at temperate latitudes, but more data will be necessary to assess whether this is truly the case and to determine the extent to which this might participate in species coexistence.

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