

Ecology of Mutualisms

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Advanced article

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Mutualisms are interactions among individuals of different species that benefit both sides and encompass a wide diversity of interspecific exchanges of resources or services. The effects of mutualisms pervade multiple levels of biological organisation. At the individual level, mutualisms provide fitness benefits for interacting partners, creating novel metabolic pathways and providing dispersal services, trophic rewards or defence against natural enemies. At the population level, the positive effects of mutualisms have the potential to increase population densities above the limits imposed by resource availability. At the community level, mutualisms form networks of interacting species that impact the persistence of local populations as well as their evolutionary and ecological dynamics. The broader implications of mutualisms to biodiversity are illustrated by the fact that mutualistic interactions are the backbone of species-rich ecological communities, such as tropical rainforests and coral reefs, and by how mutualisms fueled the spreading of humankind around the world.

individuals of different species in which there are positive net effects for both sides (Bronstein, 2009). Mutualisms are sometimes referred to as synonymous of symbiosis, especially in the marine ecology literature, but herein we will follow the broader sense adopted in the literature of terrestrial ecosystems in which symbiosis denotes that individuals of different species are under tight biological integration, no matter if interactions are mutualisms (+/+), antagonisms (+/-) or commensalism (+/0) (Douglas, 1994). See also: **Interspecific Interaction**

Mutualisms encompass a wide diversity of resource or service exchanges between species and often involve organisms that belong to disparate taxa. Indeed, some of the most conspicuous mutualisms encompass species that belong to different kingdoms and whose individuals combine abilities generating mutual benefits (Leigh, 2010). In mutualisms, species barter nutritional resources that may include water, carbohydrates, inorganic nutrients, and a variety of services, such as the movement of gametes, the transport of propagules, protection, and the removal of natural enemies (Ollerton, 2006). Mutualistic interactions are ubiquitous across aquatic and terrestrial ecosystems (Figure 1). In aquatic ecosystems, reef corals and single-celled flagellate organisms form symbiotic mutualisms in which flagellate organisms produce carbohydrates via photosynthesis, enhance rates of coral calcification and, in exchange, receive protection and obtain easy access to nutrients from the corals (Muller-Parker *et al.*, 2015). Clownfish are often associated with anemones in an interaction where the anemones benefit from the fish leftovers and the fishes gain protection of the stinging tentacles of their partners (Ricciardi *et al.*, 2010). Some shrimps and fishes clean a suite of clients that are benefited by the removal of ectoparasites and damaged tissues (Côté, 2000). Shrimp species also participate in defensive mutualisms in which a shrimp shares its burrow with a goby fish in exchange of more accurate information on predators and other threats provided by the visually oriented goby (Thompson *et al.*, 2013). See also: **Mutualism Among Free-living Species**

In terrestrial ecosystems, two of the most conspicuous mutualisms involve plant reproduction. Most plants depend on animals to pollinate their flowers, ensuring sexual reproduction. Animal pollinators include species from a variety of taxa, such as insects, birds, bats, and even nonflying mammals and lizards. Animal pollinators often benefit from resources provided by the plants, such as nectar, pollen, oils, scents, shelter, microclimatic

Mutualisms: Definition and Diversity

No organism exists alone. All organisms establish ecological interactions with individuals of other species, which can impose losses, benefits or be neutral with regards to their survivorship and reproduction. A mutualism is an ecological interaction between

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Figure 1 A few terrestrial and marine mutualisms. (a) Symbiotic mutualisms between fungi and algae form lichens that are able to colonise a variety of environments. Photo by M. A. R. Mello. (b) Workers of ant species that tend extrafloral nectaries can minimise the effects of herbivores, as illustrated by these individuals of *Camponotus rubritorax* attacking a caterpillar close to extrafloral nectaries of *Acacia constricta* (Fabaceae). Photo by W. Dátillo. (c) Clownfishes (*Amphiprion periderion*) benefit from protection provided by the tentacles of sea anemones (*Heteractis magnifica*), which in turn benefit from the fish leftovers. Photo by J. P. Krajewski. (d) Frugivorous animals, such as some bats, play a key role in plant life cycles by affecting the fate of seeds. Photo by M. A. R. Mello. (e) Pollinators, such as bees, also provide key services to plants by moving plant gametes and ensuring their sexual reproduction. Photo by M. M. Pires. (f) Cleaner species are widespread in marine ecosystems, such as this shrimp of the genus *Lysmata*, here interacting with its client, the dark-spotted moray eel *Gymnothorax fimbriatus*. Photo by J. P. Krajewski.

protection, and warming (Wilmer, 2011). After pollination, another mutualistic interaction may affect plant reproductive success by determining the fate of seeds. Seeds that fall close to the parental tree are often killed by pathogens, by seed predators or by the competition for resources with the parental tree and siblings. The majority of tropical trees and many other plant species rely upon animals – mostly birds, mammals and ants – to disperse their seeds away, a process that increases the odds of seed survival and germination (Jordano, 2000). Animals, in turn, benefit from feeding on energy-rich tissues that surround the seeds, such as pulps or arils. Plants are also involved in

a variety of symbiotic mutualisms. For example, many plants interact with nitrogen-fixing bacteria circumventing the severe growth limitation imposed by the scarcity of usable forms of nitrogen in the soil. Thousands of host plant species, including legumes, nonleguminous dicots, water-ferns and bryophytes, acquire nitrogen compounds from different groups of bacteria. On the other hand, bacterial symbionts benefit from the consumption of high amounts of the carbohydrates synthesised by their plant partners (Douglas, 1994). Most plants also form symbiotic associations with some fungi. In these associations – called mycorrhizae – plants increase the rate of absorption

of water, phosphates and other minerals, whereas fungi obtain carbohydrates produced by the plants via photosynthesis (Smith and Read, 2008). **See also: Mutualistic Symbioses**

Terrestrial mutualisms do involve disparate phylogenetic groups. For instance, the Yellow-headed caracara (*Milvago chimachima*, Falconidae) and other bird species feed on the parasites of capybaras and tapirs (Sazima, 2007). In addition, lichens are symbiotic associations between algae or cyanobacteria (the photobionts) and fungi (the mycobionts) that enable these organisms to colonise disparate habitats, from bare rock to tree trunks. Lichens are characterised by exchanges of metabolic services that encompass the provision of water and mineral nutrients by the mycobionts, the fixation of carbon dioxide into biomass via photosynthesis by photobionts and, when cyanobacteria are involved, also nitrogen fixation (Douglas, 1994). Ant species are also involved in multiple types of mutualisms, including the cultivation and dispersal of fungi on which Attini ants feed and the protection of honeydew-producing insects against natural enemies (Hölldobler and Wilson, 1998). **See also: Lichens**

Although the catalogue of mutualistic interactions described earlier is far from being exhaustive, it illustrates the wide diversity of mutualisms in nature. Mutualisms have long been recognised as remarkable examples of natural history and played a major role in the early development of evolutionary biology as well as in contemporary thinking on coevolution (reviewed in Thompson, 2005). In contrast with the central role of mutualisms in evolutionary biology, ecological theory overlooked mutualisms until recently. Fulfilling such a historical gap regarding the study of mutualistic interactions is now recognised as a major avenue of research, as the ecological effects of mutualisms pervade the levels of biological organisation. **See also: Coevolution**

At the individual level, mutualistic interactions provide key resources and services that contribute to survival and reproduction of interacting individuals. At the population level, the positive effects of mutualisms may determine the densities and persistence of local populations. At the community level, mutualisms bind together multiple interacting species to form complex networks whose structure affect the dynamics of ecological communities. In this article, we briefly describe the ecology of mutualisms across different levels of biological organisation, providing an overview of their ecological effects on individuals, populations, and communities. **See also: Positive Interactions in Community Organisation**

Mutualisms at the Individual Level: How Do Mutualistic Partners Interact?

At the individual level, an interaction is a mutualism if it increases the fitness of both interacting individuals by increasing their survival and/or reproductive success, no matter its effects at the population level (Bronstein, 2015). The positive effects of mutualisms may lead to the misconception that mutualisms are interactions in which organisms of different species behave altruistically to benefit each other. Actually, mutualisms are reciprocally exploitative interactions in which both interacting

individuals obtain net benefits often arising from the exchange of distinct resources or services (Leigh, 2010; Santamaría and Rodríguez-Gironés, 2015). **See also: Selection: Units and Levels**

Measuring the effects of ecological interactions at the individual level can be challenging. However, at least for some mutualisms, there are well-established methods to achieve that. The benefits of pollination for plants, for instance, can be measured by the amount of pollen transferred between conspecific individual plants or by the amount of seeds produced after pollination. Similarly, measures of the number of seeds deposited by animal dispersers, the proportion of dispersed seeds that germinate, and the seed transportation distance allow estimating the effectiveness of the seed dispersal service (Jordano, 2000). Conversely, in many other mutualisms, quantifying the contribution of a single interaction event to partner's survival or reproduction is harder and requires more laborious experimental work. **See also: Pollination by Animals**

The outcome of a mutualism can be so important for the organisms that some mutualisms are obligatory interactions, that is, the individuals cannot survive or reproduce without their partners. For example, some self-incompatible plants cannot reproduce in the absence of pollinators. In contrast, some mutualisms are facultative, that is, the interaction increases fitness, but they are not obligatory. An example of facultative mutualisms is the case of animals that only eventually feed on fruits. Therefore, the outcomes of mutualistic interactions often depend on the natural history of the interaction itself. Making sense of the diversity of mutualisms is challenging and, as in the case of any ecological pattern (Levin, 1992), grouping is only possible by simplifying the characterisation of mutualisms. Simplification always implies the risk of losing relevant information, but grouping may allow us gaining insights and making generalisations. In this sense, mutualisms can be grouped according to the degree of biological integration between the interacting species – the interaction intimacy (Ollerton, 2006). Variation in the levels of interaction intimacy is associated with how mutualistic partners interact and with the types of resources and services they exchange.

The variation of interaction intimacy across mutualistic systems can be understood as a continuum of morphological, physiological and/or behavioural integration between mutualistic individuals (Figure 2). At the lower extreme of the interaction intimacy continuum, the very presence of individuals of mutualistic species may result in benefit to individuals of a given species. These mutualisms result in reciprocal and positive effects, even in the absence of physical interaction and labour division (Boucher *et al.*, 1982; Leigh, 2010). The most well-known mutualism characterised by simple presence benefit without labour division is the Müllerian mimicry. For instance, unpalatable *Heliconius* butterflies of different species share similar colour patterns that predators learn to avoid. As a consequence of Müllerian mimicry, the *per capita* risk of predation decays in the presence of individuals of other (mutualist) species (Müller, 1879). Other mutualisms involve individuals of different species that move together and benefit of their distinct sensorial abilities to find prey or detect predators, without physical interaction. Examples include mixed flocks of foraging birds (Leigh, 2010)

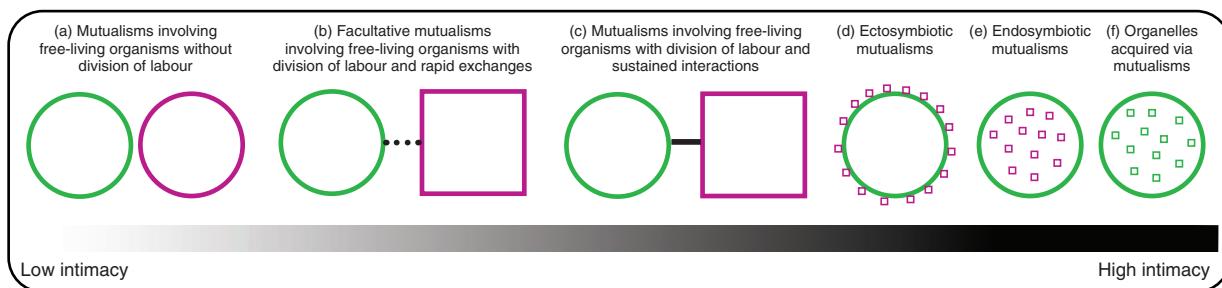


Figure 2 A schematic view of the diversity of mutualisms based on interaction intimacy. The bar at the bottom denotes increasing interaction intimacy. Geometric figures with different colours indicate different mutualist species. Squares and cycles depict labour division, that is, interacting individuals provide highly complementary resources or services to each other. (a) Mutualisms without division of labour that involve no physical interaction or exchange between free-living species, for example, Müllerian mimetism and mixed-species bird flocks in which birds forage together. (b) Facultative mutualisms between free-living organisms with division of labour. Examples include a wide variety of mutualistic associations characterised by rapid exchanges between species, such as interactions between plant and pollinators, plant and animals dispersing seeds, cleaner species and their clients and protective ants tending plants with extra-floral nectaries. (c) Mutualisms between free living species that involve sustained interactions with physical association between the species during at least the majority of the life cycle of one of the organisms, such as occur in mutualistic associations between fig and fig wasps, anemone and anemonefishes and between protective ants and their host myrmecophyte plants. (d) Ectosymbiotic mutualisms that involve interactions characterised by strong metabolic and physiological attachment between small, often microscopic symbiont and their mutualist hosts, such as occur in association between ruminants and the cellulose-digesting microbiota that inhabits the rumen. (e) Endosymbiotic mutualisms in which the symbiont lives inside the cells of their hosts, such as widespread associations between protozoans and bacteria. (f) The most extreme case of intimate mutualisms is the association between eukaryotic cells and endosymbionts that have became key intracellular organelles – the mitochondria and chloroplasts – that are genetically and metabolically integrated to the host.

and hunting associations between coyotes and badgers (Minta *et al.*, 1992). **See also: Mimicry**

Most mutualisms, however, are based on some physical contact between interacting individuals that exchange resources or services. Some mutualisms are short-term interactions. A hummingbird spends a few seconds interacting with the flowers of a given plant. Toucans spend a couple of minutes feeding on fruits of fruiting trees. Similarly, cleaner gobies would spend just a few minutes cleaning a given fish in the coral reef. In other mutualisms, physical contact lasts much longer. For example, clownfishes spend most of their lives close to a single anemone. Accordingly, some pollinating fig wasps spend a considerable part of their lifetimes physically interacting with only two fig trees. As larvae, the wasps emerge from eggs deposited by a fig wasp within the flowers of a modified inflorescence known as syconium. As adults, the female fig wasps will carry pollen from the flowers of the syconium where they were born to the flowers of a syconium of another fig tree where they can lay eggs.

Symbiotic interactions are at the upper end of the interaction intimacy continuum (**Figure 2**). In symbiotic mutualisms, interacting individuals are physically connected by persistent interactions. The bodies of the hosts, the largest individual mutualistic partners, often harbour multiple smaller individuals named symbionts. For example, many bacteria, fungi, and protozoans live in the guts of insects, birds, and mammals. These symbiotic associations allow the animal species to survive on a cellulose-rich diet. In these mutualisms, the cellulose-breaking symbionts use the plant tissues ingested by the animal host while providing digestible matter. The repeated evolution of this kind of obligate symbiotic interaction promoted the ecological success of disparate groups of animals, such as termites and ungulates. **See also: Mutualistic Symbioses**

Symbioses are associations that undeniably play a major role in the ecology and evolution of living systems. Each of the

'individuals' we identify in nature are in fact living 'arks', composed by a number of other organisms with which they interact both antagonistically (parasites) and mutualistically. Even the cells of animals, plants, and fungi carry the relicts of ancient mutualistic interactions. Examples include the mitochondria within eukaryote cells and the chloroplasts within plant cells (Margulis, 1970). Compelling evidence supports the endosymbiotic theory, which hypothesizes that the physical integration of eukaryote cells and bacteria created the kinds of organisms we now identify as the most conspicuous components of Earth's biota: animals, plants, and fungi. From an ecological perspective, by affecting survival and reproduction, mutualisms are keystone interactions shaping the demography of interacting populations. In the following section, we explore how mutualisms affect the ecology of populations. **See also: Mitochondria: Origin**

Mutualisms at Population Level: How Do Mutualisms Persist?

At the population level, mutualisms can be defined as ecological interactions that increase densities of the populations of both interacting species by reducing death rates and/or by increasing birth rates (Boucher *et al.*, 1982; Holland, 2015). Conversely, in the absence of the mutualistic partners, a population should attain smaller densities or might even be unable to thrive in the case of obligatory mutualisms. However, increased fitness benefits for individuals do not necessarily translate into larger population densities or faster population growth (Boucher *et al.*, 1982). For example, benefits at the individual level may lead to unsustainable population densities and, in the long-term, to the collapse of populations of interacting partners. Along the same lines, interactions may lead to large population densities even if

most individuals of one species undergo fitness reduction. For example, domestication by humans made the cattle (*Bos taurus*) the most abundant ruminant on Earth. Nevertheless, selective breeding imposed by humans implies that only a small subset of the individuals reproduces and most individuals (especially males) do not reproduce at all. **See also:** [Evolution during Domestication](#)

Assuming that populations are not limited by the availability of resources or by natural enemies, theory predicts that populations should grow indefinitely in an exponential manner. Mutualisms amplify the potential for this unbounded growth because the increased number of individuals in one population is expected to have a positive effect on the growth of the population of its partner. This positive feedback would thus result in the indefinite growth of both populations. Because no population can keep sustained exponential growth in nature, much of the work on the population ecology of mutualisms focusses on identifying the ecological factors that create negative feedbacks and limit the potential for unbounded exponential growth promoted by mutualisms. **See also:** [Malthus, Thomas Robert](#)

One of the mechanisms that can limit the unbounded growth expected from mutualisms is intraspecific competition. Intraspecific competition occurs when the population shows density-dependent regulation, that is, growth rates decrease when population density increases due to resource limitation. Simple models of population dynamics suggest that this unsustainable positive feedback of mutualisms can only take place if the combined positive effects of the mutualisms surpass the negative density-dependent effects of competition. Conversely, if negative density dependence is greater than the mutual benefit populations exert over each other, then the positive effect of mutualism can be counterbalanced. This implies that mutualisms should never have strong effects on population dynamics, a prediction challenged by patterns we observe in nature. Consequently, other mechanisms may be needed to explain why populations of mutualistic partners persist. **See also:** [Density Dependence and Independence](#)

One possible route to understand the persistence of populations of mutualists is to recognise that the net positive effects of mutualistic interactions are determined by the interplay between the gross benefits and the costs of the mutualism. Costs include the production of resources offered to the mutualistic partner, such as floral and extra floral nectar, carbohydrates and lipids in the pulp of fleshy fruits or glycogen-based food bodies (Müllerian bodies produced by *Cecropia* trees and consumed by their protective ants); services performed by the partner, such as the costs of carrying heavy seeds by volant animals in the stomach or the risk of predation that cleaners face when approaching clients; and negative effects on other mutualisms, such as the interference of protective ants on the pollination of their mutualistic plants. Theoretical models show that when costs are taken into account, a suite of different outcomes is possible, from stable coexistence to unstable dynamics where one species is not able to persist due to overexploitation by its partner. The outcome depends on the densities of each interacting population, the strength of the interactions and how asymmetric the benefits (and costs) for each species are. These diverse potential responses

illustrate the variety of population-level effects mutualisms may have. **See also:** [Ant-Plant Mutualisms](#)

The costs associated to mutualisms often constrain the benefits of increased numbers of partners in multiple ways. For instance, plants need time to reload flowers with nectar after pollinator visits. The addition of more visiting bees will not increase the net reproductive benefit obtained by the plant indefinitely. As in the case of nectar reload, benefits coming from additional events of mutualistic interactions can saturate due to multiple biological mechanisms. The net benefit will saturate when costs and/or gross benefits are not proportional to the densities of the mutualistic partners (Holland and DeAngelis, 2010). Consequently, the net benefit may become null or costs may overcome benefits over a density threshold. Under this scenario, population growth promoted by mutualistic partners is also expected to be bounded. **See also:** [Population Dynamics: Introduction](#)

Another consequence of the balance between gross benefits and costs is that the outcomes of mutualisms are often context-dependent. The major ecological effect of such conditional outcomes is that an interaction between the very same species can shift from mutualism (+/+) to commensalism (+/0) or antagonism (+/−). Therefore, to label an interaction ‘mutualistic’ is just an approximation that may help us to detect patterns and infer processes in nature. The conditionality of mutualisms arise from spatiotemporal variability of numerous factors, such as the spatial distribution and density of the mutualistic partner, the abundance of competitors and predators, nutrient availability, and demographic properties of the interacting populations, such as age classes (Bronstein, 2009). Conditional outcomes are expected to be more common when the benefits depend on the abundance of the partner, in contrast to mutualisms in which a single partner individual is able to provide the resources or services needed for the mutualistic exchange (Bronstein, 2015).

Mutualisms also allow the persistence of cheating lifestyles that exploit interactions (Bronstein, 2001). Examples of cheaters include flower visitors that obtain the nectar without touching the reproductive structures of the flower and birds that consume pulp without dispersing seeds but obtain the resources available in the fleshy pulp avoiding the costs of carrying seeds. The exploited partner still has to deal with the costs of the mutualism but acquire few or no benefit. The cost of exploitation imposed by cheaters can decrease the growth rate of the populations, controlling population densities. Consequently, exploiters and mutualistic partners can coexist under equilibrium dynamics where the exploiter damps the growth of the mutualist population (Ferriere *et al.*, 2002; Wang *et al.*, 2012; **Figure 3**). Other types of ecological interactions, such as competitive interactions among species that share partners, or predation, also affect ecological dynamics and may prevent unbounded population growth. **See also:** [Parasitism: The Variety of Parasites](#)

In contrast to the large amount of theoretical work on mutualisms, empirical studies examining how mutualisms shape population dynamics in nature are relatively scarce. All processes listed earlier may act simultaneously to regulate natural populations. More empirical studies can unravel which of these mechanisms are major forces allowing the coexistence of multiple mutualistic partner species. What we know is that many mutualisms form species-rich assemblages that persist across

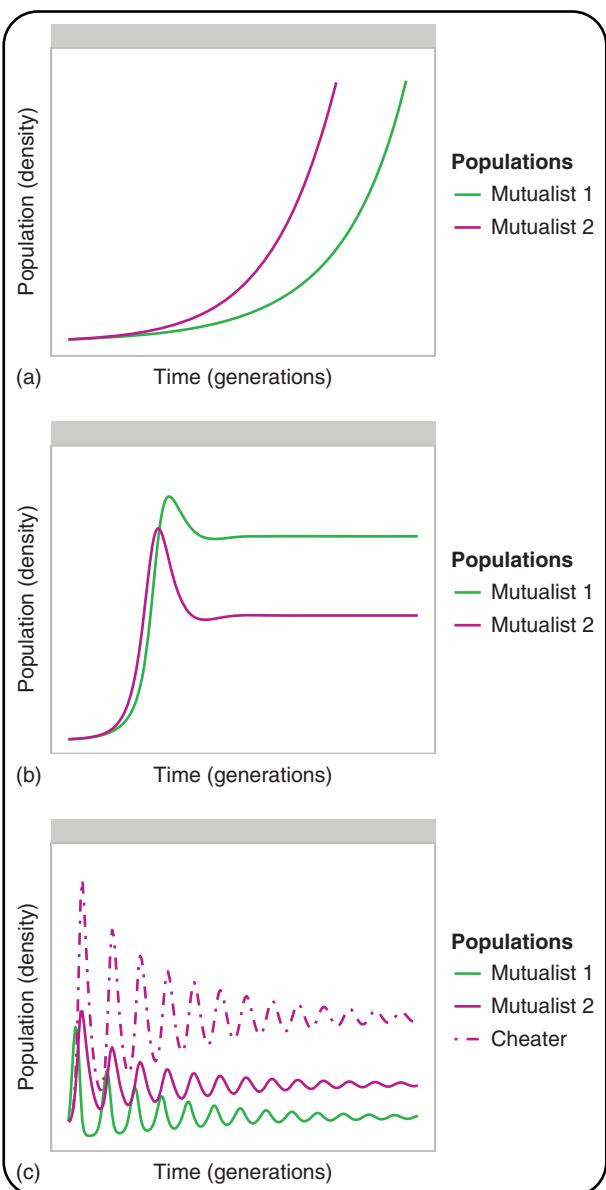


Figure 3 Theoretical populations dynamics between mutualists. (a) The positive effects of mutualism between two populations lead them to exponential growth, resulting in unbounded densities. (b) The positive effect of mutualism is limited by saturation of the benefit gained, resulting in bounded population densities. After a given threshold of mutualistic partner density, the interaction does not convert into population growth, reaching the density equilibria of both populations. (c) The presence of cheaters in one of the populations limits the benefit the other population may gather with the interaction. The negative (or null) effect of cheaters bounds the density of the partner that in turn regulates the density of the mutualistic partners and cheaters. Populations oscillate until reaching the equilibria of bounded densities of coexistence of mutualists and cheater.

time. In this sense, to understand the persistence of multispecific mutualisms may depend, at least in some level, on responses for the question of how the persistence of populations is affected by the interconnected nature of ecological communities. See also: [Coexistence](#)

Mutualisms at Community Level: How Do Mutualisms Form Networks?

In textbooks, mutualisms often appear as examples of reciprocal specialisation, in which a pair or few mutualistic species interact with each other. A classic example is the pollination of the orchid *Agraecum sesquipedale* studied by Charles Darwin, whose flowers hide the nectar in a long and narrow spur that can only be accessed by moths with morphologically compatible proboscis. This system, among many others studied over the years, popularised the notion that mutualisms often involve highly specialised morphological, physiological or behavioural traits. Such a notion fostered the interest in highly specialised pairwise interactions.

The focus on reciprocal specialisation is also at the root of the widely used concepts of pollination and seed-dispersal syndromes. In the context of animal–plant mutualisms, a syndrome is a set of plant characteristics that presumably represent adaptations related to interactions with a certain group of partners (Faegri and van der Pijl, 1976; van der Pijl, 1982). For instance, hummingbirds are usually assumed to pollinate large-sized flowers that are conspicuously coloured, generally towards red, whereas small-sized flowers, usually white or yellow, or of any colour able to reflect UV light (invisible to human eyes) are assumed to rely on pollination by bees. Although in some cases syndromes may lead to reasonable guesses on interaction partners, exceptions are frequent enough to support the notion that syndromes should not be used as a predictive tool that replaces observation (Jordano, 1995; Ollerton *et al.*, 2009). See also: [Coevolution; Pollination by Animals](#)

Along the same lines, the idea that specialisation is ubiquitous in mutualisms has been losing ground. Species-specific associations are more common in intimate mutualisms between highly interdependent species, such as in obligate mutualisms between symbionts and their hosts. Nevertheless, even some interactions that used to be considered extremely specialised, such as the interactions between yuccas and yucca moths or between figs and fig wasps, often seem to involve more than only two mutualist species (Waser *et al.*, 1996). Accordingly, in mutualisms among free-living species, such as most pollination and seed dispersal by animals, the richness of interacting partners can be variable across species (Boucher *et al.*, 1982). In fact, Waser *et al.* (1996) have shown that most species are moderately generalised in plant-pollinator mutualisms, and the same applies to many other interactions, including coral-zooxanthellae associations and lichens (Stanton, 2003). Although extreme degrees of specialisation do occur in nature, they are likely to be the exception rather than the rule, as each pairwise interaction is embedded in mutualistic networks containing multiple interactions that connect one

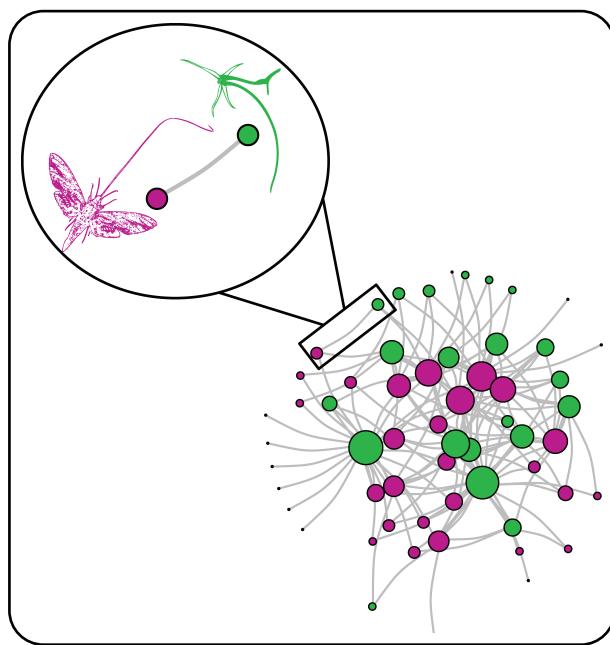


Figure 4 Mutualistic interactions are embedded in complex interaction networks. Even species that show a high degree of morphological specialisation such as some hawk moths (Sphingidae) and orchids (Orchidaceae) that often establish interactions with other species in the community. In the theoretical plant-pollinator network depicted here species are represented as nodes and links represent interactions between them. The size of each node is proportional to the number of interactions each species establish.

species to many other (Figure 4). See also: **Community Ecology: An Introduction**

Because mutualisms are part of larger interconnected systems, a more in-depth understanding of their consequences requires more than the study of pairwise interactions in isolation (Stanton, 2003). Currently, ecologists interested on mutualisms borrow tools from other disciplines, such as social sciences, physics, and the study of food webs, to characterise the structure of mutualistic networks. Networks quantitatively describe the arrangement of interactions and allow the investigation of how their structure affects ecological dynamics and shapes evolution (Bascompte and Jordano, 2013). In the past two decades, the large amount of empirical and theoretical works focussing on mutualistic networks has made mutualisms a model system for exploring the relationships between structure and functioning in ecological networks. See also: **Food Webs**

Network analysis allowed some general patterns to be unravelled in mutualisms. Because most species interact with a limited set of partners, only a small portion of the possible interactions do occur, that is, the connectance of mutualistic networks is often low. However, a few species may have a disproportionately large number of interactions (Bascompte and Jordano, 2013) and be highly central to network structure, whereas many others have fewer interactions and occupy a peripheral position within the network (Bascompte and Jordano, 2013). When we consider the frequency or the strength of interactions, most interactions seem to be asymmetric, at least in low intimacy mutualisms

(Bascompte *et al.*, 2006). For example, some plants rely upon a few very large mammals such as tapirs for seed dispersal. In contrast, tapirs feed on fruits of dozens of species at any given site.

Network studies also revealed that mutualistic interactions are not randomly distributed across species and may actually form complex patterns. In highly intimate mutualisms, such as ant–myrmecophyte and anemone–anemone fish interactions, networks are often organised as semi-independent species subsets called modules (Fontaine *et al.*, 2011). In a modular network, interactions are much more frequent within than between the species subsets (modules). Some low intimacy species-rich networks, including some seed-dispersal (Donatti *et al.*, 2011) and plant-pollinator networks (Olesen *et al.*, 2007), may also display modular structure. However, low intimacy mutualisms are usually characterised by a nested structure (Fontaine *et al.*, 2011). Nested networks are characterised by interactions among species in which those species with fewer interactions are connected to a proper subset of the partners of highly connected species, resulting in an asymmetric overlap.

The ecological and evolutionary processes leading to modularity and nestedness may be diverse. Modularity may emerge from morphological or physiological constraints that create forbidden links between certain species. For example, large-seeded plants cannot be dispersed by small-sized birds, whereas large frugivores may prefer to consume large fruits, thus creating modules where small frugivores are preferentially associated to small-seeded plants and modules formed by large frugivores and the large-seeded plants they disperse (Donatti *et al.*, 2011). Alternatively, modularity may emerge if certain sets of species are more likely to overlap in space or time than others.

Nestedness may also be generated by multiple processes, including the variation in abundances among potentially interacting species, higher coextinction rates of reciprocal specialists and variation in traits that allow a species to interact with many other species (Vázquez *et al.*, 2009). For instance, plants flowering for long periods may end up interacting with a wide range of pollinators, whereas plants that flower for short time intervals will only interact with pollinators that are active at those intervals. Plants whose flowers allow easy access to nectar may interact with many pollinators, whereas those that have very restrictive morphology may limit the number of partners. Therefore, different mechanisms may be responsible for the structural patterns observed in mutualistic networks.

The structure of mutualistic networks may have consequences for the ecological dynamics of mutualisms. For instance, nestedness has been associated with the robustness of mutualistic assemblages to extinctions (Memmott *et al.*, 2004). The nested structure is characterised by a core of species with many interactions, which may allow species to persist even when some of their partners go locally extinct. On the other hand, nested mutualistic networks may be sensitive to the extinction of highly connected species. The modularity of mutualistic networks can also affect community dynamics such that high modularity appears to reduce the persistence of mutualisms over time (Thébaud and Fontaine, 2010). Theoretical work has also shown that species-rich mutualistic networks are expected to be less responsive to perturbations (Okuyama and Holland, 2008). Yet, recent work has shown that highly connected mutualistic networks may be more likely to

undergo cascades of extinctions after one species is lost (Vieira and Almeida-Neto, 2015). When considered in the context of larger networks that include interactions such as competition and predation, mutualisms seem to favour community maintenance (Mougi and Kondoh, 2012). At the same time that mutualisms between individuals scale up generating networks at the community level, these networks may have important implications for the survival of individuals and the persistence of populations involved in mutualistic interactions.

Concluding Remarks

Mutualisms represent cornerstones for the most diverse ecological communities on Earth. Most of the energy that flows across the components of coral reef communities is the result of the mutualistic interaction between corals and their mutualistic, photosynthesising symbionts. Experiments have shown that cleaning interactions maintain a high diversity of coral reef fishes. On the other hand, protective ants can lead a single plant species to take over formerly high diverse patches of rainforest forest (Frederickson *et al.*, 2005). Most of plant species rely upon pollinators for sexual reproduction and more than 70% of woody plants in the Tropics and between 30% and 50% in temperate regions depend on animals for seed dispersal (Jordano, 2000). Lichens are fundamental for the ecological succession in many temperate ecological communities. Much of the nitrogen and phosphorus available for life in terrestrial ecosystems is the result of the interaction among plants, rhizobia and mycorrhizae. Therefore, mutualisms are fundamental for the maintenance of biodiversity and ecosystem functioning.

The relevance of mutualisms for humankind is also pervasive. Mutualistic interactions actually supported the success of humankind in spreading and becoming the dominant species across the planet. Our key mutualistic partners were species that are now very abundant and cosmopolitan, such as dogs, horses, cattle, chicken, wheat, yeast, maize, and rice. We established cooperative hunting groups with dogs that allowed us to obtain prey that were previously inaccessible. We now rely on mutualisms with plant crops that cannot reproduce without human's farming them for food and with mammalian herbivores we raise and protect against natural enemies. Even the human microbiota – the collection of symbiotic parasites and mutualists that live within our bodies – control multiple aspects of our health. We are now just beginning to understand the pivotal role of mutualisms in shaping not only the biodiversity at multiple scales, but humankind itself.

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References

- Bascompte J, Jordano P and Olesen JM (2006) Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* **312**: 431–433.
- Bascompte J and Jordano P (2013) *Mutualistic Networks*. Princeton: Princeton University Press.
- Boucher DH, James S and Keeler KH (1982) The ecology of mutualism. *Annual Review of Ecology and Systematics* **13**: 315–347.
- Bronstein JL (2001) The exploitation of mutualisms. *Ecology Letters* **4**: 277–287.
- Bronstein JL (2009) Mutualism and symbiosis. In: Levin SA (ed) *The Princeton Guide to Ecology*. Princeton: Princeton University Press.
- Bronstein JL (2015) *Mutualism*. Oxford: Oxford University Press.
- Côté IM (2000) Evolution and ecology of cleaning symbioses in the sea. *Oceanography and Marine Biology: An Annual Review* **38**: 311–355.
- Donatti CI, Guimarães PR, Galetti M, *et al.* (2011) Analysis of a hyper-diverse seed dispersal network: modularity and underlying mechanisms. *Ecology Letters* **14**: 773–781.
- Douglas A (1994) *Symbiotic Interactions*. Oxford: Oxford University Press.
- Faegri K and Van der Pijl L (1976) *Principles of Pollination Ecology*. Oxford: Pergamon Press.
- Ferriere R, Bronstein JL, Rinaldi S, Law R and Gauduchon M (2002) Cheating and the evolutionary stability of mutualisms. *Proceedings of the Royal Society of London B* **269**: 773–780.
- Frederickson ME, Greene MJ and Gordon D (2005) Ecology: 'Devil's gardens' bedevilled by ants. *Nature* **437**: 495–496.
- Fontaine C, Guimarães PR, Kefi S, *et al.* (2011) The ecological and evolutionary implications of merging different types of networks. *Ecology Letters* **14**: 1170–1181.
- Holland JN and DeAngelis DL (2010) A consumer-resource approach to the density-dependent population dynamics of mutualism. *Ecology* **91**: 1286–1295.
- Holland JN (2015) Population ecology of mutualisms. In: Bronstein JL (ed) *Mutualism*. Oxford: Oxford University Press.
- Hölldobler B and Wilson EO (1998) *The Ants*. Springer.
- Jordano P (1995) Angiosperm fleshy fruits and seed dispersers – a comparative-analysis of adaptation and constraints in plant-animal interactions. *American Naturalist* **145**: 163–191.
- Jordano P (2000) Fruits and frugivory. In: Fenner M (ed) *Seeds: The Ecology of Regeneration in Plant Communities*, 2nd edn. Wallingford: CABI Publishing.
- Leigh EG Jr, (2010) The evolution of mutualism. *Journal of Evolutionary Biology* **23**: 2507–2528.
- Levin SA (1992) The problem of pattern and scale in ecology. *Ecology* **73**: 1943–1967.
- Margulis L (1970) *Origins of Eukaryotic Cells*. New Haven: Yale University.
- Memmott J, Waser NM and Price MV (2004) Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society B* **271**: 2605–2611.
- Minta S, Minta K and Lott D (1992) Hunting associations between badgers (*Taxidea taxus*) and coyotes (*Canis latrans*). *Journal of Mammalogy* **73**: 814–820.
- Mougi A and Kondoh M (2012) Diversity of interaction types and ecological community stability. *Science* **337**: 349–351.

- Müller F (1879) *Ituna and Thyridia*; a remarkable case of mimicry in butterflies. *Transactions of the Entomological Society of London* **1879**: 20–29.
- Muller-Parker G, D'Elia CF and Cook CB (2015) Interactions between corals and their symbiotic algae. In: Birkeland C (ed) *Coral Reefs in the Anthropocene*. Dordrecht: Springer Science + Business Media.
- Okuyama T and Holland JN (2008) Network structural properties mediate the stability of mutualistic communities. *Ecology Letters* **11**: 208–216.
- Olesen JM, Bascompte J, Dupont YL and Jordano P (2007) The modularity of pollination networks. *Proceedings of the National Academy of Sciences of the United States of America* **104**: 19891–19896.
- Ollerton J (2006) "Biological barter": patterns of specialization compared across different mutualisms. In: Waser NM and Ollerton J (eds) *Plant Pollinator Interactions: From Specialization to Generalization*. Chicago: University of Chicago Press.
- Ollerton J, Alarcón R, Waser NM, et al. (2009) A global test of the pollination syndrome hypothesis. *Annals of Botany* **103**: 1471–1480.
- Ricciardi F, Boyer M and Ollerton J (2010) Assemblage and interaction structure of the anemonefish-anemone mutualism across the Manado region of Sulawesi, Indonesia. *Environmental Biology of Fishes* **87**: 333–347.
- Santamaría L and Rodríguez-Gironés MA (2015) Are flowers red in teeth and claw? Exploitation barriers and the antagonist nature of mutualisms. *Evolutionary Ecology* **29**: 311–322.
- Sazima I (2007) Unexpected cleaners: Black Vultures (*Coragyps atratus*) remove debris, ticks, and peck at sores of capybaras (*Hydrochoerus hydrochaeris*), with an overview of tick-removing birds in Brazil. *Revista Brasileira de Ornitologia* **15**: 417–426.
- Smith SE and Read DJ (2008) *Mycorrhizal Symbiosis*, 3rd edn. New York: Elsevier.
- Stanton M (2003) Interacting guilds: moving beyond the pairwise perspective on mutualisms. *American Naturalist* **162**: S10–S23.
- Thébaud E and Fontaine C (2010) Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* **329**: 853–856.
- Thompson JN (2005) *The Geographic Mosaic of Coevolution*. Chicago: Chicago University Press.
- Thompson AR, Adam TC, Hultgren KM and Thacker CE (2013) Ecology and evolution affect network structure in an intimate marine mutualism. *American Naturalist* **182**: E58–E72.
- Vázquez DP, Blüthgen N, Cagnolo L and Chacoff NP (2009) Uniting pattern and process in plant–animal mutualistic networks: a review. *Annals of Botany-London* **103**: 1445–1457.
- Van der Pijl L (1982) *Principles of Dispersal in Higher Plants*, 3rd edn. Berlin: Springer.
- Vieira MC and Almeida-Neto M (2015) A simple stochastic model for complex coextinctions in mutualistic networks: robustness decreases with connectance. *Ecology Letters* **18**: 144–152.
- Wang Y, Hong W and Sun S (2012) Persistence of pollination mutualisms in plant–pollinator–robber systems. *Theoretical Population Biology* **81**: 243–250.
- Waser NM, Chittka L, Price MV, Williams NM and Ollerton J (1996) Generalization in pollination systems, and why it matters. *Ecology* **77**: 1043–1060.
- Wilmer P (2011) *Pollination and Floral Ecology*. Princeton: Princeton University Press.

Further Reading

- Bascompte J and Jordano P (2013) *Mutualistic Networks*. Princeton: Princeton University Press.
- Boucher DH, James S and Keeler KH (1982) The ecology of mutualism. *Annual Review of Ecology and Systematics* **13**: 315–347.
- Bronstein JL (2015) *Mutualism*. Oxford: Oxford University Press.
- Douglas A (1994) *Symbiotic Interactions*. Oxford: Oxford University Press.
- Karplus I (2014) *Symbiosis in Fishes: The Biology of Interspecific Partnerships*. Hoboken, NJ: Wiley-Blackwell.
- Thompson JN (2005) *The Geographic Mosaic of Coevolution*. Chicago: Chicago University Press.