

Pathways to mutualism breakdown

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Mutualisms are ubiquitous in nature despite the widely held view that they are unstable interactions. Models predict that mutualists might often evolve into parasites, can abandon their partners to live autonomously and are also vulnerable to extinction. Yet a basic empirical question, whether mutualisms commonly break down, has been mostly overlooked. As we discuss here, recent progress in molecular systematics helps address this question. Newly constructed phylogenies reveal that parasites as well as autonomous (non-mutualist) taxa are nested within ancestrally mutualistic clades. Although models have focused on the propensity of mutualism to become parasitic, such shifts appear relatively rarely. By contrast, diverse systems exhibit reversions to autonomy, and this might be a common and unexplored endpoint to mutualism.

The evolutionary pathways of mutualism and the potential for breakdown

Mutualisms are fascinating because not only do they involve traits in one species that benefit individuals of other species [1], but the maintenance of these interactions is also difficult to reconcile with natural selection [2–4]. Selection shapes organisms to maximize individual fitness and conflicts of interest are expected to arise whenever non-relatives interact [2–4]. Such conflicts pose a challenge for the maintenance of mutualisms because each partner might benefit most from either exploiting or abandoning the other [5–9]. Pollination is a classic and easily observed example: flowering plants often benefit from animal pollinators that transmit plant gametes and receive nectar in exchange. However, some plants have abandoned the partnership for wind or self-pollination [10], while others have evolved empty flowers that cheat pollinators of nectar [11]. Meanwhile, some plant visitors have evolved to rob nectar without pollinating the plant [12]. An important goal of theory is to understand what maintains mutualism stably over time.

The study of mutualisms is currently undergoing a revolution as scientists increasingly understand them to be taxonomically and ecologically pervasive [13,14]. Research on microbes represents an important component of this increased attention: it is now widely recognized that plants and animals commonly harbor a spectrum of microbial mutualists, including bacteria, algae or fungi [14–25]. Associations between microbes and plant or animal hosts have often been distinguished as symbioses and considered separately from other interspecific interactions [15,18].

Symbioses are defined as intimate interactions among different species [15,18], and some are renowned as extreme and ancient cases of cooperation, such as bacterially derived organelles (e.g. mitochondria), which have had a fundamental role in eukaryote evolution [26]. However, results from empirical research have blurred distinctions between beneficial symbioses and other mutualisms. Microbes exhibit many characteristics that are shared by other types of mutualists, including facultative interactions [18], free-living life-history stages [15], mutualistic interactions with multiple partner lineages [27], and a potential to cheat their partners [25,28].

Most empirical work and theory has focused on the specific conditions and mechanisms that maintain mutualism [2–9,13,25,28–42]. Here, we explore the alternative case, the breakdown of mutualism, which we define as those evolutionary transitions that terminate a mutualism (i.e. the loss of cooperative phenotypes in a lineage of mutualists over time).

Predicting mutualism breakdown

Three main predictions exist about the breakdown of mutualisms. The first and oldest prediction is that mutualisms are vulnerable to extinction [31,32,43,44]. Lotka–Volterra models have revealed some fundamental characteristics of persistent mutualisms, and these apply especially to obligate partnerships. In particular, each partner population must exhibit growth above a minimal level in the presence of their partner species, and this positive effect on growth eventually saturates when populations become large [31,32,45]. When these conditions are not met, obligate mutualist populations can go extinct, and this might commonly be the case in fluctuating environments [8,31,32,45]. If mutualists are facultative, populations can be stable irrespective of partner population size [32].

A shift to parasitism

The second prediction is that mutualism can shift to parasitism. Selection shapes mutualists to obtain maximum benefits from their partners and parasitic individuals can supplant cooperative ones [2–5,9,13,29,34,37,42,43,46]. Parasites are individuals that receive benefits from partners without reciprocation, and are often termed cheaters or exploiters [46]. Two models predict selective conditions that might maintain mutualism by preventing shifts to parasitism [4,42].

The first model is byproduct mutualism, in which the cooperative trait(s) of a mutualist involves minimal or zero fitness costs [4,30,33,36,42]; examples include bird feathers or insect scales that transfer pollen (and benefit a

visited plant) as an automatic consequence of their structure. If this trait comes without a fitness cost to the pollinator, there might be little selective potential for the pollinator to benefit further by not pollinating the plant when collecting nectar.

The second model is reciprocity, in which cooperative benefits directed from one individual to another are returned to the first for a net fitness benefit [29]. Reciprocity has two mechanisms. Partner fidelity involves long-term or repeated interactions among partners that promote correlated fitness interests between them [2–4,29,34,37,42], such as microbial mutualists that are vertically transmitted in a host lineage [2–4,13,34]. Partner choice or sanctions occur when an interacting party is able to alter its response based on the behavior of the other [3,4,28,38,40–42]; for example, legumes sanction rhizobial symbionts that produce insufficient nitrogen for the plant, perhaps by decreasing the photosynthate supply to the uncooperative rhizobia [28].

Shifting cost:benefit ratios

The third prediction is that the cost:benefit ratio of mutualisms can shift over time and favor a return to autonomy for one partner [8,14,47], which we term abandonment of mutualism. The cost:benefit ratio of a mutualism can become unfavorable if mutualist partners are difficult to find [47]; if available partners are a poor match [14]; if unrelated third parties disrupt reciprocity by parasitizing the mutualism [6,7]; or if the benefits received from mutualists become accessible cheaply from the environment [18,48]. For instance, it is widely known that the effectiveness of mutualists can be altered by environmental conditions so that they are beneficial to partners in only some conditions [46]. Nutritional mutualisms illustrate this well; one partner produces a key metabolite in exchange for protection, housing or other service from a second partner [46]. If the metabolite provided by the first partner becomes freely available in the environment, the second partner might realize a net benefit from abandoning the interaction. For instance, plants that form nutritional root symbioses with arbuscular mycorrhizal fungi can opt out of the symbiosis in rich soils [48]. Likewise, legumes that are usually nodulated by nitrogen-fixing rhizobia can bypass such interactions when mineral nitrogen is plentiful [19].

A related scenario occurs when mutualists shift to alternative partners that provide higher levels of benefit [39]. However, unlike abandonment, partner switching is not a breakdown of mutualism within a lineage. The selective conditions that favor abandonment of a mutualism are similar to those for parasitism in one respect: the costs of the interaction outweigh the benefits for one partner. However, in parasitism, one partner gains fitness benefits at a cost to the other; the costs that favor abandonment by one partner do not benefit the other partner.

How might mutualisms break down?

Few predictions exist about how any particular type of mutualism might break down. Are some mutualist lineages more likely to go extinct, shift to parasitism or abandon the interaction? One challenge to addressing this question empirically is that the breakdown of a mutualism

might occur via two or more steps. In particular, if a mutualism has shifted to parasitism, the parasitized partner might subsequently evolve to abandon the costly interaction [8,47] or might go extinct [44]. The ecology of the interaction, as well as the degree of options available to each partner, are crucial in shaping these transitions. Once a mutualism has evolved, the capacity for independence can become either limited or lost [49]. Obligate mutualists, for instance, might get trapped with a parasitizing partner or be pushed to extinction. However, if partners can readily cease interacting (i.e. the interaction is facultative), then abandonment might result even from mild exploitation [47].

Phylogenetic evidence: putting mutualism theory to the test

Two phylogenetic approaches have been used to investigate the macroevolution of interacting lineages. One compares phylogenies, the other analyzes single-lineages. Mutualistic interactions are known to be complex, often involving multiple partner species and partner switching [1,6,7,13–15,18,39,46], and one method of unraveling this complexity is to compare the evolutionary histories of interacting lineages using co-phylogenies [50]. Co-phylogenetic studies often analyze whether there is co-speciation among interacting lineages [20,21,51] and can provide information about partner specificity and partner switching [20,21,50,52,53]. However, they offer limited information about the evolution of the interaction if the phylogenies under study exhibit little congruence, and this might commonly be the case [50].

The approach that we focus on here studies the evolution of single lineages of mutualists, without regard to their interacting partners. The evolutionary processes that maintain or break down cooperation are thought to act separately on each species in an interaction [4], hence it is possible to study the evolution of cooperative interactions from a one-sided perspective. The single lineage approach involves reconstructing a phylogeny that includes mutualists and related taxa, mapping mutualist, non-mutualist and parasite traits onto the tree, and using ancestral state reconstruction [54] to infer transitions from mutualism to parasitism (Figure 1) and mutualism to autonomy (Figure 2). This approach must be used with caution, because the quality of phylogenetic evidence can vary greatly and some data sets only imply the occurrence of mutualism breakdown.

Limitations to the single lineage approach

There are four main limitations to this approach. First, classifying taxa as autonomous, mutualistic or parasitic is challenging. Detailed natural history information or fitness assays are required to classify taxa correctly and this information is not always available. Second, inference of evolutionary histories relies on accurate ancestral state reconstruction based on a well resolved phylogeny [50], and if either is incorrect it might produce spurious hypotheses of evolutionary transitions [54]. Third, evolutionary histories inferred from molecular data only rarely reveal extinction. Testing hypotheses about extinct lineages is difficult, and the remaining species are likely to represent

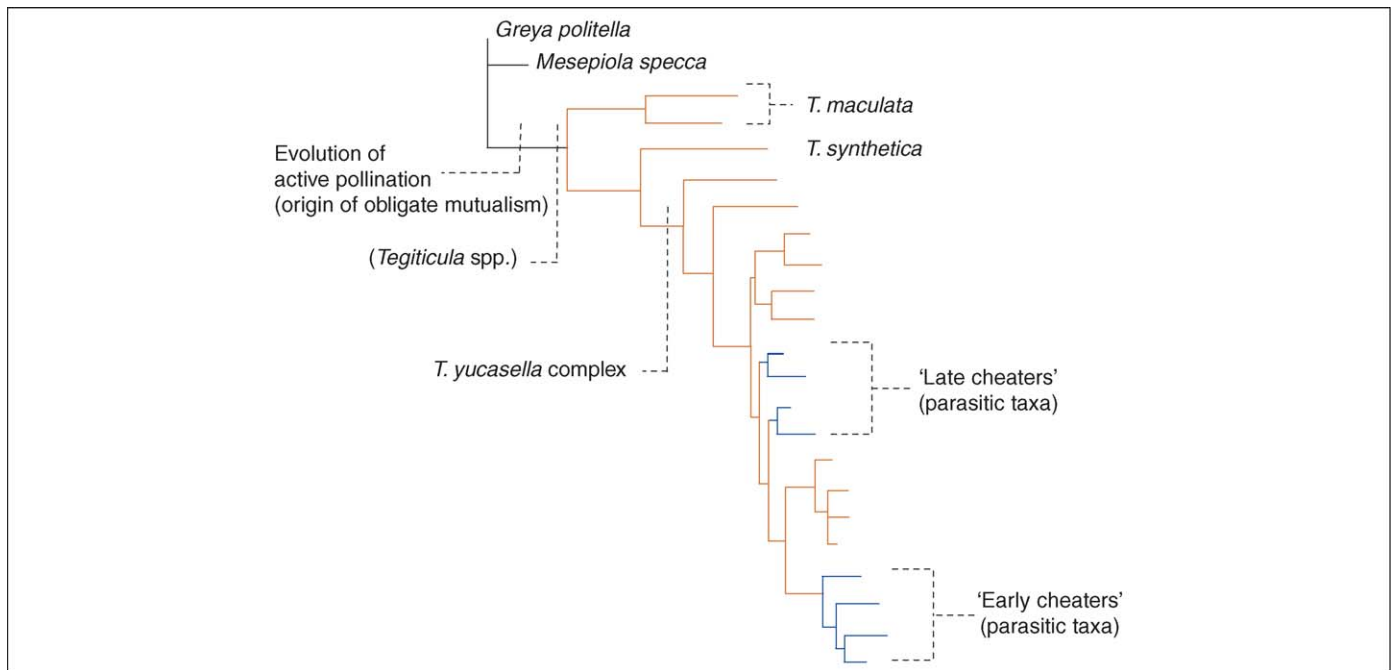


Figure 1. Phylogenetic relationships among yucca moths estimated using maximum parsimony from 2.1-kb of mitochondrial DNA sequence. The yucca moths *Tegeticula* spp. form obligate interactions with host plants in the genus *Yucca*. The moths lay their eggs into the fruit or flowers of the host plant and the larvae subsequently feed on the developing seeds. Pollinating taxa, indicated with red branches, are obligate mutualists with the host plant. Non-pollinating taxa, indicated in blue, are parasites of their plant hosts, and depend on other yucca moth species to pollinate their hosts. Non-pollinators (or 'cheaters') oviposit into fruits at two different phenological stages, either early or late during the development of the fruit. The outgroup taxa, *Greya politella* and *Mesepiola specca*, do not exhibit active pollination and are indicated with black branches. A parsimony analysis estimates either two or three evolutionary origins of parasitism in the yucca moths [52]. Reproduced with permission from [52].

a biased subset of taxa. Finally, phylogenies are unlikely to uncover standing polymorphism. Transitory coexistence of mutualists, parasites and non-mutualists within a species might easily get overlooked, especially if only few individuals are sampled.

Evidence for mutualism breakdown

Empirical data generated with the single lineage approach suggests that mutualism breakdown has occurred in diverse lineages (Table 1). For instance, recent data suggest that diverse lineages of saprophytic (free-living) fungi are nested within ancestrally mutualist clades [16,55], free-living strains of cyanobacteria are nested within lineages that form mutualisms with fungi [27], free-living euphorb trees are nested within clades that form obligate mutualisms with ants [56] and insect seed-parasites of plants are nested within clades of pollinating mutualists [52,53]. Strikingly, even the eukaryotic-organellar 'mutualism', a hallmark example of extreme and ancient cooperation between species [13,26], shows evidence of breakdown: the eukaryote lineages in *Trypanosoma* and *Entamoeba* have evolved autonomy from chloroplast and mitochondrial mutualists, respectively [57,58].

Mutualist clades that lack evidence of mutualism breakdown appear only in obligate partnerships. Examples include insect agriculture, in which ants and termites have independently evolved to 'farm' fungi, as well as mutualistic bacterial endosymbionts that infect diverse insect clades [51]. In these examples, transitions to parasitic or non-mutualist taxa have not been detected in the interacting lineages [20,21,51]. Here, we examine in detail

the different classes of transitions, both predicted and observed.

Extinction of mutualists

The role of extinction in mutualism breakdown has been studied using population models [31,32,43,45]. Theoreticians disagree over the vulnerability of mutualists to extinction [45], and few empirical methods exist to test hypotheses about extinction or its rate among taxa. A variety of factors unrelated to mutualism can increase rates of extinction within a lineage, including body size and geographical range [59], and methods must distinguish such background extinction from excess extinction among mutualists. One phylogenetic survey of mutualist taxa is consistent with predictions of increased extinction risk in some mutualisms; obligate mutualisms were found to be concentrated within more 'recent' clades [44]. However, obligate mutualisms might not be representative of the broad diversity of mutualisms [1,6,46].

For example, obligate mutualists are often thought to be constrained from switching partners [52], which might increase their risk of extinction subsequent to partner loss [44]. Facultative mutualisms, however, often involve beneficial interactions among multiple potential partners [6] and extinction of one mutualist population might be of little significance in the long term [32]. If one facultative mutualist population goes extinct, surviving partners can expand secondary associations or switch to new associations after the extinction. For instance, one theoretical study of pollination networks simulated loss of pollinators and observed which plants were left non-pollinated [60]. Many of the plant species investigated were found to have

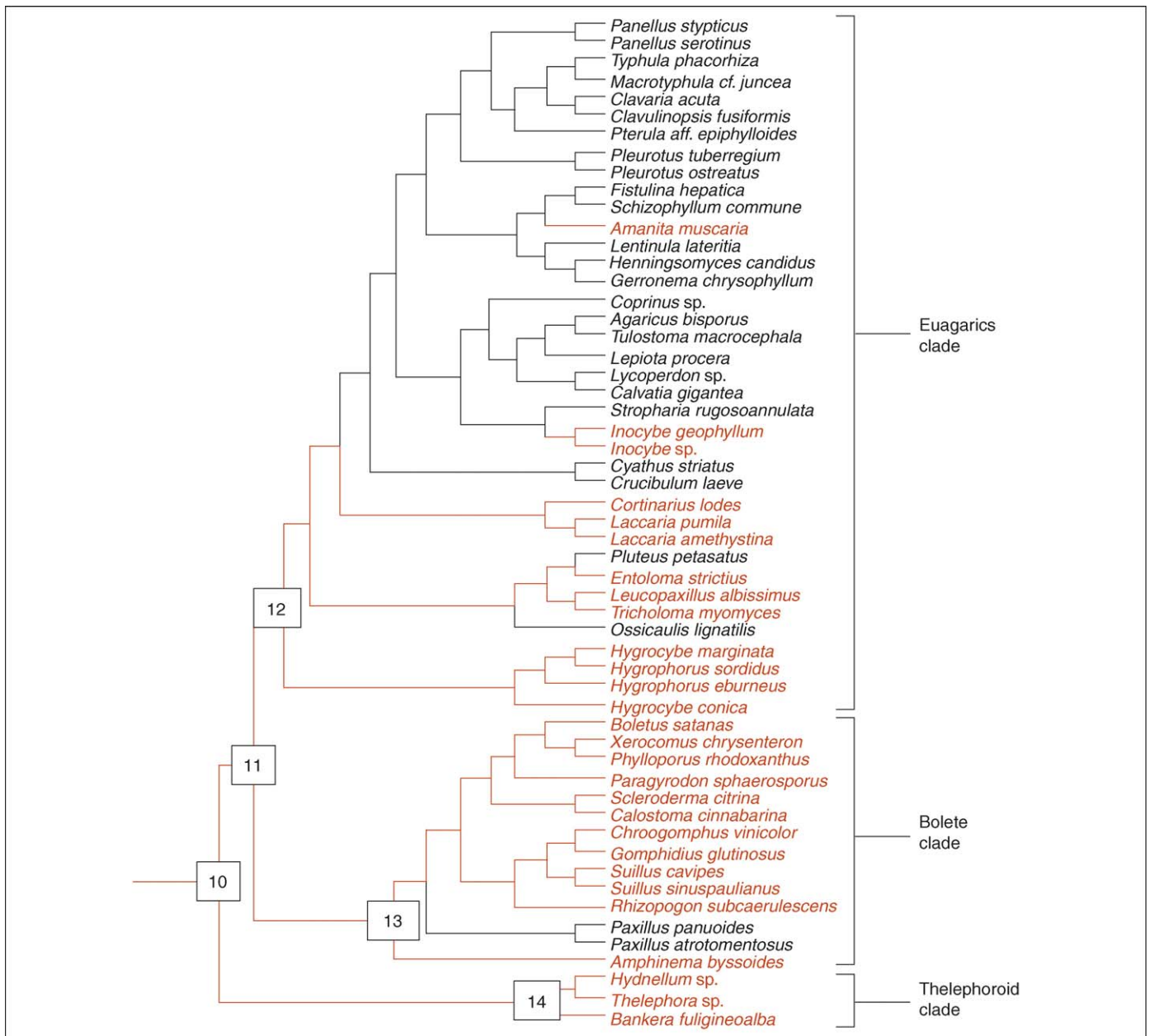


Figure 2. Mutualism and autonomy mapped onto a phylogeny of homobasidiomycete fungi inferred from 3.2 kb of aligned rDNA [16]. Ectomycorrhizal fungi form symbiotic relationships with plants in which the fungi obtain photosynthates from the plant in exchange for mineral nutrients and are assumed to be beneficial to plant hosts [16]. Only detailed fitness analyses will reveal if this is always the case. One clade from the analysis by Hibbett *et al.* [16] is shown here, including the euagarics, bolete and thelephoroid sub-clades [16]. The estimated ancestral state is ectomycorrhizal (indicated with red branches). The nodes labeled 10–14 were estimated to be ectomycorrhizal using maximum likelihood. Non-ectomycorrhizal (autonomous) taxa, indicated with black branches, emerge multiple times within the ancestrally ectomycorrhizal clade. The analysis of Hibbett *et al.* [16], including taxa not shown here, used a parsimony-based ancestral state reconstruction and estimated 3–9 losses of the ectomycorrhizal habit in homobasidiomycete fungi. However, one challenge to this conclusion is that the number of inferred losses of the mutualism is sensitive to the topology of the phylogenetic estimate [16]. Reproduced with permission from [16].

redundant interactions with multiple pollinators, and this minimized the risk of plant extinction caused by pollinator loss [60].

Shifts from mutualism to parasitism

The bulk of theory modeling the stability of mutualism predicts that it is vulnerable to erode into parasitism [2–5,9,13,29,34,37–40,42,43,46]. Hence, it is surprising that only a handful of empirical studies have discovered such shifts [52,53,61,62] (Table 1). Two unambiguous examples come from pollination mutualisms. Specialized, obligate pollination mutualisms occur between figs and fig wasps

[53] as well as between yuccas and yucca moths [35,52]. In both mutualisms, pollinating insects oviposit into the ovaries of the plant and deposit pollen in those flowers. The insect larvae subsequently feed on a subset of the developing seeds [35,52,53]. In some cases, sanctions by the plant can select against pollinator exploitation because flowers with high pollinator-egg load are abscised by the plant [35]. However, parasites that lay their eggs into flowers without pollinating them have evolved in at least two separate lineages of yucca moths [48], (Figure 1), and in one species of fig wasp [53]. In all cases, parasites are likely to have evolved only after their ancestors colonized a

Table 1. Phylogenetic studies of mutualism and its breakdown

Mutualism	Description of breakdown	Events	Refs
Evolution of autonomous taxa nested within mutualistic clades			
Plant–pollinator	Wind-pollinated plant taxa emerge within angiosperms that are ancestrally animal pollinated	>5 ^a	[10]
Fungal–plant	Saprophytic fungi nested within a clade of fungi that form mutualisms with herbaceous and woody plants	3–9 ^b	[16]
<i>Wolbachia</i> –nematode	Mutualism with <i>Wolbachia pipientis</i> symbionts gained and/or lost multiple times across a clade of nematodes	~6 ^a	[24]
Lichen	Free-living Cyanobacteria nested within clades of lichen symbionts	~1–4 ^a	[27]
Lichen	Free-living (saprophytic) fungi nested within clades of lichenizing fungi	3–4 ^b	[55]
Ant–plant	Myrmecophily gained and/or lost multiple times across a lineage of host plants	≥1 ^b	[56]
Eukaryote–organellar	Secondary loss of mitochondrial organelles in <i>Entamoeba</i>	1 ^a	[57]
Eukaryote–organellar	Secondary loss of plastid organelles in <i>Trypanosoma</i>	1 ^a	[58]
Algal–invertebrate	Free-living algae in the genus <i>Gymnodinium</i> emerge within a clade that forms mutualistic symbioses with marine invertebrates	1–2 ^b	[64]
Algal–invertebrate	Octocorals lacking symbiotic algae nested within a clade of symbiotic hosts	≥1 ^b	[65]
Aphid–ant	Mutualism with ants (myrmecophily) gained and/or lost multiple times across a genus of aphids	~1–5 ^b	[66]
Evolution of parasitic taxa nested within mutualistic clades			
Yucca–yucca moth	Multiple seed-parasitizing species of yucca moth nested within a clade of obligately yucca-pollinating mutualists	2 ^b	[52]
Fig–fig wasp	A seed-parasitic wasp species nested within a clade of obligately fig-pollinating mutualists	1 ^b	[53]
Fungal–plant	Monotrope plants that parasitize root fungi nested within clades of plants that are fungal mutualists	1 ^b	[61]
Butterfly–ant	Butterfly taxa that parasitize ants nested within clades that are ant mutualists	1 ^b	[62]
Examples of ancient mutualisms without evidence of breakdown			
Ant–fungus	Ancient agricultural mutualism in which ants farm fungi	0 ^b	[21]
Termite–fungus	Ancient agricultural mutualism in which termites farm fungi	0 ^b	[19,20]
Aphid– <i>Buchnera</i>	Ancient mutualism between aphids and their endosymbiotic bacteria, <i>Buchnera</i>	0 ^b	[51]

^aNumber of mutualism breakdown events inferred from referenced paper.

^bNumber of mutualism breakdown events estimated in referenced paper.

novel host that already had a pollinator. All non-pollinating parasites coexist with pollinating species, and coexisting pairs on a host are not sister taxa [35,52,53].

A shift to parasitism has occurred in mutualisms between root-infecting fungi and terrestrial plants. Many land plants form mutualisms with fungi through direct contact between roots and fungal hyphae, termed mycorrhizae [48]. Plant hosts benefit fungi via photosynthetically derived carbon and, in exchange, the fungi often offer a variety of fitness benefits to plants [18,48]. However, some non-photosynthetic plant species have evolved to take carbon from root fungi [61]. The Monotropoideae (Ericaceae) are a lineage of achlorophyllous plants that parasitize their mycorrhizal fungi. Parasitism of the fungi has evolved once in the plant family Ericaceae, as other members of the family appear to form the typical mutualism with mycorrhizal fungi [61]. This shift to parasitism is similar to the fig wasp and yucca moth examples above in that there is a three-way interaction: the parasite (the achlorophyllous plants) coexists with cooperative plant species on the fungus [61]; such three-way interactions appear to help maintain newly evolved parasites [6,7,52].

The elegant mutualism between large blue butterflies (Lycaenidae) and ants has shifted into parasitism [62,63]. The larvae of most lycaenid butterflies provide nutritious secretions to ant mutualists in exchange for their protection [63]. However, ant parasitism has evolved within a clade of mutualist butterflies: larvae of the lycaenid genera *Phengaris* and *Maculinea* either prey on ant brood, are ‘cuckoos’ that are fed by ant workers, or mix different parasitic strategies [62]. Although more than 30 butterfly species in these genera exhibit various forms of ant parasitism, phylogenetic reconstruction suggests only a single

shift to parasitism [62]. Other shifts to parasitism have probably occurred in ant-associated butterflies and are yet to be documented in detail. Ant-parasitic traits appear broadly distributed across the lycaenid and riodinid families of butterflies, both of which contain many ant-mutualist species, suggesting a potential for frequent shifts to parasitism and little phylogenetic constraint against such shifts [63]. However, only a small proportion of the known parasitic butterflies have been analyzed phylogenetically to see whether they are nested within mutualistic clades [62,63]. Experts in the field suggest that once these shifts occur, parasitism on ants is often short-lived evolutionarily as parasitic taxa appear prone to extinction [63].

Abandonment of mutualism

Evidence of mutualists reverting to autonomy appears in the phylogenetic records of diverse interactions (Table 1), from marine mutualisms [64,65] to lichens (symbiotic partnerships in which cyanobacterial or algal ‘photobionts’ live inside fungi [27,55]). Multiple lineages of angiosperm plants, presumed to have animal-pollinated ancestors, have switched to wind pollination or self-pollination [10]. In some mutualisms, evolutionary shifts to autonomy have occurred separately in each partner class. For example, in algal–invertebrate mutualisms, free-living dinoflagellate algae have evolved from within mutualist algal lineages [64] and octocoral hosts have evolved autonomy from their algal mutualists [65]. Similarly, in lichens, some fungal lineages have returned to an autonomous existence [55], as have some photobiont lineages [27].

In some lineages in which mutualists have shifted to autonomy, there is evidence that the interaction might

Box 1. Outstanding questions

- What traits or ecological conditions enable or constrain shifts between mutualism and parasitism and between mutualism and autonomy? To uncover the traits or conditions that promote or constrain such shifts, comparative analyses could investigate taxa that have shifted to parasitism or abandoned mutualism.
- Shifts from mutualism to parasitism or autonomy might increase extinction risk in the taxa that have made these shifts. Which process is more likely to result in extinctions of mutualist partner species, shifts to autonomy or shifts to parasitism? Field and laboratory manipulations could test these hypotheses.
- What is the evolutionary history of third-party species that exploit mutualists? Parasites of mutualisms appear common in nature [6,7], but do third-party exploiters often evolve from one of the partners of a mutualism or do they usually represent unrelated clades that have diversified via exploitation of mutualist taxa?
- Are reversions to ancestral states more likely than to novel states? For instance, if the ancestor of a mutualist is a parasite, is a reversion to parasitism more likely than a shift to autonomy?

New research avenues

The increasing discovery and understanding of microbial mutualists is opening new avenues for research. Experimental evolution of microbial mutualists can test hypotheses about the selective forces that govern shifts between mutualism and non-mutualism, and detailed genetic analyses can test hypotheses about genetic mechanisms that regulate or constrain shifts. The following questions can be addressed with microbial mutualists:

- Do shifts to parasitism or abandonment of mutualism occur via irreversible genetic pathways, such as gene loss [17]? Laboratory evolution experiments could manipulate mutualisms and investigate such shifts empirically.
- Do shifts from mutualism occur via a few mutations of large effect or are many mutations required? Phylogenetic studies that identify evolutionary shifts from mutualism should foster genomic work that elucidates the genetic mechanisms behind the shifts.
- Is lateral transmission of mutualism-specific genes a common pathway to mutualism breakdown? One suggestion has been that shifts between mutualism and parasitism in bacteria might primarily occur by lateral transmission of symbiosis islands and/or pathogenicity islands [22]. Rhizobial bacteria provide an excellent test case: mutualists, parasites and autonomous taxa are all interspersed, and the genes that express mutualistic as well as pathogenic characters are known to be transmissible among genomes [23].

have offered only weak benefit to one partner. Octocorals that have evolved loss of algal symbionts are an example: as efficient filter-feeders with low surface:volume ratios, octocorals might benefit little from nutrition provided by algae, as compared with other host taxa [65]. Similarly, it has been suggested that, in host plants that harbor ants, the plants shift to autonomy because the benefits of hosting ants are low [66]. Abandonment might be particularly common in nutritional mutualisms, especially when one partner can acquire the benefit from the environment. For example, in plant-microbial mutualisms, evolutionary reversion to autonomy would be expected in host plants that experience more competition for light than for soil-borne resources.

Are shifts to parasitism rare?

There appears to be a paucity of phylogenetic evidence for shifts to parasitism. Of the four taxa in which mutualism has shifted to parasitism, three probably exhibit one evolutionary origin [53,61,62], whereas the other exhibits two or three [52]. However, cases of abandonment appear more common and often have multiple evolutionary origins

(Table 1). Several artifacts could create this pattern. First, the pattern might arise from a small or biased sample of studies. The number of studies highlighted here is relatively small because the empirical test requires a well resolved phylogeny and accurate classification of mutualistic, parasitic and autonomous taxa. A bias could be created if investigators were more likely to research abandonment of a mutualism than a shift to parasitism, but this seems improbable.

A second explanation is that shifts to parasitism might be transient, and recorded in the phylogenetic record only under restrictive conditions. Theory modeling shifts to parasitism between two species suggests that the emergence of parasitism in one of the partner species could drive the other species to extinction [43,52]. Indeed, in four of the five independent origins of parasitism that we highlighted [52,53,61] (including both lineages of yucca moths), parasites coexist with mutualist species that might have prevented extinction of the parasitized partner. Shifts to parasitism would also be short lived if parasitized partners abandon the interaction [47]. In point of fact, all five shifts to parasitism occurred in obligate mutualisms [52,53,61–63], where abandonment is unlikely.

Finally, shifts to parasitism could truly be rare. Two genetic mechanisms have been suggested that support this theory. The first states that mutualist and parasite lifestyles involve distinct pathways of genome evolution, such as differential gene loss [17]. Data from bacterial phylogenies support this hypothesis in that mutualist and parasitic bacterial taxa are deeply diverged [17]. Another hypothesis is that stable cooperative traits can exhibit pleiotropy that constrains parasitism [67]. Future empirical investigation of mutualism breakdown should address these and other related questions (Box 1).

Conclusions

A main assumption of mutualism theory is that cooperation between species is vulnerable to erode into parasitism. However, phylogenetic data provide only scant evidence of parasitic shifts. Instead, phylogenetic evidence suggests that evolutionary shifts to free-living states occur across diverse mutualist clades. Cost:benefit analysis makes a clear prediction about when evolutionary shifts to autonomy are favored, and one fruitful avenue will be to test these hypotheses via comparative phylogenetic approaches and with experimental evolution (Box 1).

We have described two alternative hypotheses for the rarity of shifts from mutualism to parasitism. The first is a genetic constraint hypothesis and predicts that shifts from mutualism to parasitism are constrained by gene loss [17] and/or pleiotropy [67]. One laboratory experiment successfully selected for parasitism in populations of algal mutualist of jellyfish [25]. However, the parasitism was relatively mild [25] and some form of genetic constraint might explain this. The second hypothesis suggests transient parasitism, in which secondary shifts to abandonment or extinction obliterate the phylogenetic footprint of parasitic species. Experimental systems in which parasitism is induced or selected in the laboratory would be one way to test the transience hypothesis and further elucidate whether abandonment or extinction can result. Finally, we

have undoubtedly failed to uncover all cases of mutualism breakdown in the literature. However, we hope that we have encouraged other biologists to explore this interesting topic further.

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