HOW MUTUALISM EVOLVED IN NATURE: THE CASE OF ANT–PLANT INTERACTIONS

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Certain species of ants and plants are seen to interact with each other in ways that benefit both. In a world of constant competition and struggle for survival, how does one explain the prevalence of such non-combative, non-competitive, and seemingly friendly interactions?

Have you ever noticed a butterfly or bee pollinating a flower? Do you know that the plant gives the insect a meal of nectar and pollen in return for this service? Philosophers from the time of Herodotus and Aristotle have observed such bizarre 'friendships' in nature. Another example is of the plover rooting around the open jaws of a crocodile. Why do you think it doesn't get eaten up by the crocodile? Because the bird picks and eats juicy blood-sucking leeches from the crocodile's mouth (see **Fig. 1**).

Are you wondering why such observations seem bizarre? Species interact with each other in myriad ways (see **Box 1**). However, most such interactions are antagonistic — either one species ends up becoming food for another species,

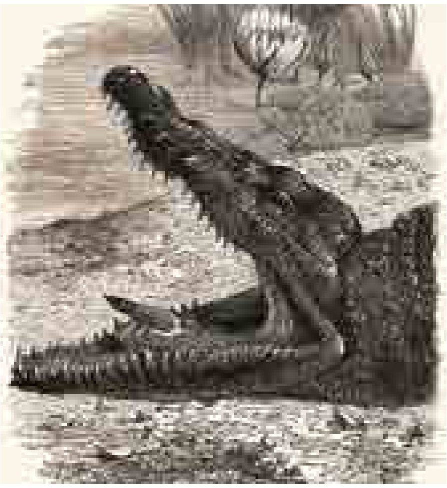

Fig. 1. A small bird, like a plover, feeds on leeches from the open mouth of a crocodile.

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Box 1. What are some other kinds of interspecies interactions?

Here are some that you may have observed in your own home or backyard —

- **Antagonism:** one organism against another like in predator–prey relationships. For example, a grasshopper feeding on grass.
- **Competition:** two or more organisms competing for the same limited resources, such as food. For example, lions and hyena competing for killed prey.
- **Commensalism:** only one party benefits from the interaction while the other is unaffected. For example, house lizards are safe from predation in the safety of human homes, while humans are not significantly affected by them.
- **Parasitism:** one party benefits at the cost of another. For example, a variety of microbes cause diseases in plants, animals, and humans.

or has to compete with it for limited resources such as food and shelter. An inter-species interaction where the two interacting species benefit each other is called **mutualism**. But why do such interactions exist?

The puzzle of mutualism

As the evolutionary biologist Dobzhansky (1973) famously said, 'nothing in biology makes sense except in the light of evolution'. According to Charles Darwin: *'... if it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory, for such could not have been produced through natural selection...'* As a result of Darwin's theory, competition and predation came to be seen as key drivers of evolution (see **Box 2**). On the face of it, one may assume that mutualisms would not be evolutionarily successful. After all, why would natural selection favor organisms that help others?

Today, we know that mutualisms exist because they are actually forms of mutual exploitation that involve a delicate equilibrium of costs and benefits (see **Box 3**). This means that for every 'give' in such friendships, there is a 'take' that recovers the cost of what is given and more. In other words, rewards are given in exchange for services rendered. Since rewards are a costly investment:

- An individual that gives the smallest possible reward in return for a particular service is likely to be more successful than one who offers more. For example, a plant that produces just enough nectar to attract insect pollinators is likely to conserve more resources for its survival and reproduction than a plant that produces an excess of nectar.
- The friendship will survive only as long as both parties reap a net benefit from it. For example, nectar production in many plant species stops as soon as the flower is pollinated.
- Such friendships are sustained only as long as the benefit for each party exceeds its costs. Any imbalance, such as cheating (yes, cheating is a technical term in ecology!), in this equation could lead to its breakdown. For example, some flowers falsely advertise nectar to attract pollinators, but don't provide this reward. Pollinators are smart — they quickly learn to avoid cheater flowers.

Mutualistic interactions are, therefore, not as genial as one imagines them to be. Not surprisingly, cheating does still work, but only when cheaters are a small fraction of a population of honest mutualists.

Box 2. Are competition and predation key drivers of evolution?

In his paradigm shifting book, 'On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life', Darwin proposed that all organisms present on earth today possess traits that have helped them survive threats in the past.

Individuals that are better at escaping predation, more efficient at competing for scarce resources (such as food or mates), or more capable of adapting to a changing environment have a higher chance of survival and reproduction. Since their progeny are likely to inherit these traits, and be better at surviving similar contexts, the 'better' trait will spread within the population. Darwin called this process **natural selection**.

Over a period of many generations, the continuous selection of traits that allows a population to adapt more successfully to a challenging environment could even lead to the **evolution** of a species that is very different from its ancestor.

Box 3. Mutualism is of two types — obligate and facultative:

In an obligate mutualism, the two partners evolve so closely together that they cannot exist without each other. For example, each species of the fig tree provides shelter to a specific wasp species that pollinates it.

Facultative mutualisms are more opportunistic. For example, some plants can be pollinated by multiple species of bees and butterflies; and many of these bee and butterfly species pollinate flowers of many different plant species. Neither partner in these mutualisms is entirely dependent on the other.

Mutualisms in ant–plant interactions

The term 'mutualism' to describe inter-species interactions that were beneficial to both species was coined in 1873, by the Belgian biologist Pierre-Joseph van Beneden. Studies on mutualism were mostly based on natural history observations till 1966-67, when Daniel Janzen, an evolutionary ecologist, experimentally demonstrated that certain species of Acacia trees and ants in Central America depended on each other.

We now know of many more plants, mostly from the tropics, that form mutualistic interactions with ants. Such ants protect the plant against herbivory.

The plants, called **ant-plants**, reward the ant with shelter and/or food:

- Ant-plants that **only** provide food rewards to their ant partners are called **myrmecophiles** (= myrmeco: ant related + phile: loving). These rewards take the form of extrafloral nectar (or EFN) and food bodies. EFN is secreted from non-floral parts such as leaf stalks, leaf laminas, and bracts. Solid food globules are secreted from the tips of leaflets or the base of leaf stalks.
- Ant-plants that **also** provide shelter to their ant partners are called **myrmecophytes** (= myrmeco: ant related + phyta: plants), and the shelters are called **domatia.** Domatia are formed by spontaneous modifications of plant parts like leaves, thorns, or branches (see **Box 4**). For example, some domatia consist of branches that are hollow on the inside and swollen up on the outside.

Since ants do not reside on myrmecophiles, they forage on these ant-plants opportunistically and, therefore, may or may not protect it. In contrast, the constant presence of ants on myrmecophytes means that they are more likely to protect their plant partners against herbivory. But is this the only way in which these mutualistic interactions may vary? Are there other selection pressures that can influence the delicate balance of costs and benefits that drive mutualistic associations? Let's explore this question through three examples.

Case I: Ant–plant interactions in bull's horn acacia

The most famous of these mutualistic associations is seen between the Central American tree *Acacia cornigera* and ants belonging to the genus *Pseudomyrmex* (see **Fig. 2**). The tree provides shelter to the ants in the form of huge hollow thorns (which give the tree its common name — bull's horn). It also provides food in the form of both EFN and food bodies (called Beltian bodies in honour of Thomas Belt who first noticed them in the 1800s). The resident ants patrol the tree day and night, and aggressively guard it against herbivory. For example, they have been observed to bite and drive away caterpillars and bigger insects from feeding on leaves. These ants have also been seen to cut off trespassing vines that try coiling around the host tree.

This ant–plant association is not only an example of obligate mutualism, but also of coevolution (see **Box 5**). Janzen's studies show that the host tree becomes fatally vulnerable to herbivory if *Pseudomyrmex* ants are experimentally removed from them. Therefore, the more ferocious the ants that are attracted to it, the better protected the tree is against herbivory. The greater the rewards (shelter and food) provided by the host tree, the more attractive the tree becomes to these ants. The more aggressive an ant, the more likely it is to out-compete other ants in finding shelter and food on the host tree. It is through these reciprocal selection pressures that coevolution has helped maintain this obligate mutualism.

Box 4. What is NOT a domatia?

Have you seen those big ant nests, made of leaves, on the mango tree in your garden? They are not domatia. The leaf nests on mango are stitched together by weaver ants, whereas domatia are ready-made shelters provided to ants by their plant partners.

Box 5. What is coevolution?

It is a process where two interacting species reciprocally influence each other's evolution through the process of natural selection. In mutualistic relationships, this process can lead to a stronger partnership over time.

Case II: Ant–plant interactions in the *Haasige mara*

Another interesting ant–plant association is seen, closer home, in the *Humbodtia brunonis* (colloquially referred to as the *Haasige mara*) — a small tree endemic to a thin belt of rainforest going north to south along the Western Ghats.

Fig. 2. An *Acacia cornigera* branch showing thorns (domatia) and yellow food bodies on tips of its leaflets. This plant was growing at the Botanical Garden in Gottingen University, Germany.

Like *Acacia cornigera*, the *Haasige mara* provides its ant partners with domatia in the form of swollen hollow branches with ready-made entrances, and food in the form of EFN on the leaves and bracts of flower buds (see **Fig. 3**). However, this mutualism is different from that of the bullhorn acacia in some important ways:

1. Only some individuals of this tree species provide domatia. Therefore, the *Haasige mara* is better described as a semi-myrmecophyte.
2. A number of ant species (~16 species) have been found to nest in the domatia of this tree species throughout its distribution range.
3. Only one ant species, called *Technomyrmex albipes*, has been found to offer any protection to the tree.
4. The domatia of this tree species host invertebrates other than ants. The most interesting of these is a peculiar 'tree-earthworm' called *Perionyx pullus*, that has been seen only in the domatia of this tree (see **Fig. 4**).

The obvious question is — does protection from herbivory have any influence on this ant–plant association? A study of the *Haasige mara* across its distributional range showed us that trees to the south were more commonly occupied by the protective ant species. A greater number of these trees showed domatia. They also produced larger volumes of EFN, with higher concentrations of amino acids. This is significant because an earlier study suggests that the protective ant species shows a preference for EFN with amino acids; whereas non-protective species feed on any EFN, as long as it is sweet. Not surprisingly, we also found that herbivory pressure was highest on trees to the south. The presence of ants significantly reduced herbivory on these trees, confirming a protective role. In contrast, the threat of herbivory and, therefore, the need for protection by ants, was lower among trees in the northern range.

Fig. 3. *Humboldtia brunonis* offers both shelter and food to ants. (a) Domatium with self-opening slit. (b) Extrafloral nectar on leaves.

Fig. 4. The arboreal earthworm *Perionyx pullus* inside a domatium of *Humboldtia brunonis*.

But our most interesting discovery was the fact that about one-fifth of the nitrogen on a domatia-bearing branch came from ants — protective and non-protective. This explains the presence of domatia and extrafloral nectar on trees to the north where the herbivory pressure is so low that investing in protection by ants may be too costly. Nitrogen is a crucial nutrient for plants, and tropical rainforest soil (where the *Haasige mara* grows) shows poor nitrogen availability. It also explains the presence of the earthworms — we found that, at any given time, about 9% of the nitrogen in a domatia-bearing branch was derived from its excreta! The tree absorbs nitrogen from the earthworm's decomposing excreta through the walls of the domatia. Scanning electron microscope (SEM) images revealed that the inner walls of domatia were lined with a mat of fungal hyphae, which could help in the breakdown of ant and earthworm excreta (see **Fig. 5**). This means that the non-protective invertebrates on *Haasige mara* are mutualists, and not freeloaders or parasites as we had previously believed. In return for the food and shelter it provides, the host plant receives nutrition from these inhabitants.

This is not only the first known example of a nutrition-based mutualism, it shows that such mutualisms could evolve alongside, or even in the absence of, protection-based mutualisms.

Case III: Non-mutualistic ant–plant interactions

Do ants always form protection- or nutrition-based mutualistic associations with plants? Not true. You can see a different kind of association in your own garden — one that is, in fact, a step more complicated than the *Haasige mara* example.

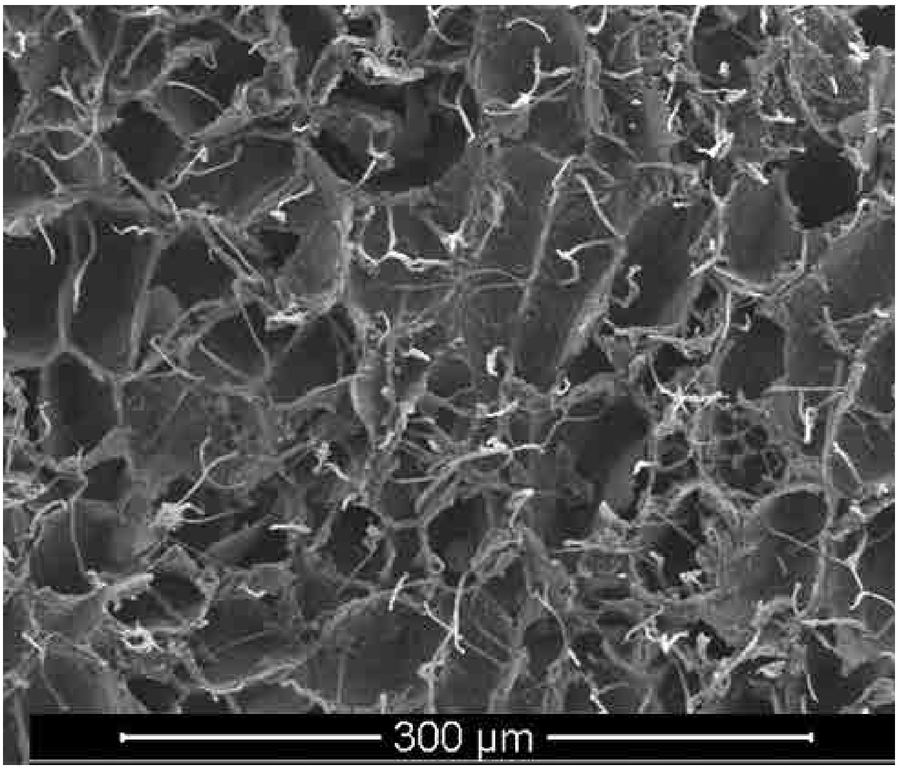


Fig. 5. **An SEM image of fungal hyphae lining the inner wall of a domatium of *Humboldtia brunonis*.**

Fig. 6. **Ants tending aphids on a plant.**

If you have ever done some gardening, you may have been in the unpleasant situation of seeing your plants being attacked by tiny insects such as aphids, scale insects, and mealy bugs. These insects use their syringe-like mouthparts, called stylets, to suck phloem sap from plants. Phloem sap, as you know, is nutrient-rich food made by photosynthesis and transferred to various plant parts to provide energy for growth and reproduction. The sap-suckers retain the amino-acids from the phloem sap, and excrete most of its sugars. The excreted sugar is in the form of sweet-droplets, called honeydew. Honeydew sounds and tastes sweet — but, remember, it is aphid poop!

Often, you will also see some ants on these infected plants. If you think that they may protect your plants against the sap-suckers, think again! Quite a few of these ant species form mutualistic alliances with the sap-suckers. Ants love honeydew, lapping it up as soon as each droplet is excreted. In return for this treat, the ants groom and clean the sap-sucking insects, much like cowherds tending their cows (see **Fig. 6**). Without this care from ants, the honeydew that collects around sap-feeder colonies invites fungal infections that present themselves as black blotches on the insects and their host plants. Ultimately, such insect colonies and their hosts tend to succumb to the fungal infection.

The protection that ants offer sap-suckers does not, however, extend to the host plant. The continued loss of phloem and the open wounds created by the sap-sucker stylets make the plant increasingly vulnerable to other pathogens. In contrast, even the amino acid-poor EFN in the *Haasige mara* trees to the north of its range serves to distract ants from tending to sap-suckers. This could be because ants are known to prefer the simpler sugars of the EFN to the more complex sugars in honeydew.

Parting thoughts

Mutualistic interactions are widely prevalent in nature. In the 'struggle for survival' that drives organisms to adapt and evolve, often with aggression and competition, some organisms have evolved the ability to participate in give-and-take interactions.

Since they improve the chances of survival and reproduction of both interacting partners, mutualisms are favored by natural selection. For example, *Acacia cornigera* offers an aggressive ant species food and shelter in return for protection against herbivory. On the other hand, *Humboldtia brunonis* offers food and shelter to many species of ants and some invertebrates, in return for both protection and nutrition. In this case, the quality and quantity of rewards provided by the host plant depend on the intensity of the threat of herbivory they face. In contrast, the case of phloem-feeding insects and their attendant ants is an example of how some mutualistic interactions between two species can happen at the cost of a third species.

These are just a few of the many examples of mutualism that are abundant around us (see **Box 6**). Can you identify some mutualistic interactions in your neighbourhood? All you'll need is a little bit of curiosity and some time to observe life more closely.

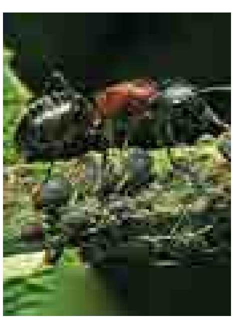
Box 6. Teacher's toolkit:

Take students on a walk in the garden to see if they can identify plants that attract ants. In particular, look for common flowering plants, like *Passiflora* spp. with extrafloral nectaries on their leaf stalks.

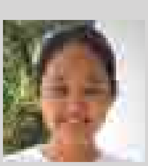
- Do ants come to feed on them?
- Is the EFN produced only in young leaves vulnerable to herbivory? Or is it produced even in mature and toughened leaves? Why?

Also look for ants tending aphids or other sap-sucking insects on plants. If you notice black soot-like smudges on these plants, observe them carefully to see if the sap-suckers and their stray honeydew are the culprits.

Key takeaways



- Mutualisms are favoured by natural selection because they are forms of mutual exploitation that involve a delicate equilibrium of costs and benefits for both interacting partners.
- Interacting partners in a mutualistic relationship can coevolve by reciprocally influencing each other's evolution.
- Ant–plant interactions offer some interesting examples of mutualism. Plants can provide food and/or shelter to ants. Ants can offer protection and/or nutrition in return.
- Some mutualisms between two species exist at the cost of a third species.
- *Humboldtia brunonis* is the only well-studied myrmecophyte (or plant that offers food and shelter to its ant partner) in India. If I were you, I would head off to the Western Ghats to see it at the earliest opportunity!



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