and are not inherited. In that sense, kleptoplasts could also be considered enslaved plastids that heterotrophs exploit in some way.

Where to go with kleptoplasty? Despite being one of the most curious endosymbioses, kleptoplasty is maybe the least understood. As a future challenge, it will be necessary to quantify the nutritional support provided by kleptoplasts to their heterotrophic hosts. What are these alien organelles good for if not boosting metabolism? In addition, it will be important to understand the evolution of kleptoplasty in order to answer one of the most important questions: Why are not all heterotrophs stealing chloroplasts to become photosynthetic?

Where can I find out more?

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DECLARATION OF INTERESTS

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Quick guide

Mistletoes

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What are mistletoes? Technically speaking, two features define a mistletoe. The first is that they do not grow from seedlings that germinate in the soil — rather they grow from seedlings that germinate on the aerial parts of another plant (Figure 1). The second feature is that mistletoes are above-ground parasites of other plants that fall into the Santalales order, also know as the sandalwoods. Above-ground or aerial parasitism has likely evolved at least five different times independently within the Santalales. So, while all mistletoes are sandalwoods, not all mistletoes are each other's closest evolutionary relatives among all the sandalwood species. It gets even more complicated, because there are also root parasites among the sandalwoods that don't 'count' as mistletoes because they don't tap into the stems, and so they are not aerial parasites. Still, there are 2,428 described species of parasitic sandalwoods, most of which are mistletoes. The vast majority of mistletoe species are found in tropical forests, as we would expect, given that most shrub and tree species — their hosts — are found in these latitudes too.

In practice, all mistletoes are still capable of photosynthesizing, but species vary widely in their ability to do so. Therefore, they are hemiparasitic, as opposed to holoparasitic. This flexible 'hemi' life history allows them to pivot between autotrophic and heterotrophic, which comes in handy when the host might be lagging in moving nutrients through their tissues. However, dwarf mistletoes are more dependent on the host for nutrients than many of the large mistletoe forms most of us have seen in shrubs and trees.

More generally, if we think about what it means to be a parasite, three conditions must be met, whether it's in a tapeworm or a mistletoe. First, parasites are intimate associates of hosts and live in or on a host (or in its nest) to complete part or all of the life cycle. Second, parasites must obtain nutrients from the host, and this must come at the host's expense. Third, parasites 'consume' hosts in units less than one individual — as opposed to predators and parasitoids, which consume their hosts in units of one. Another fundamental feature of most parasite species, whether a tapeworm or a mistletoe, is that they tend to be distributed in an aggregated way among hosts — most hosts don't harbor many parasite individuals, but a few hosts harbor most of the parasite individuals in the overall population. This distribution can be modeled using the negative binomial distribution.

How do they tap into their hosts? The embryo germinates on the host stem. Remarkably, the tiny shoot hypocotyl then moves away from light and towards gravity, contrary to most plants, and so turns toward the branch and away from the sun. As the hypocotyl hits the stem surface, a flat structure then forms upon contact between the host and parasite and a glue is secreted, which creates a holdfast. The parasite grows further into the host stem until it reaches the cambium and then stops. However, a mistletoe meristem is therefore established in the host stem and the mistletoe continues to grow there, but its annual growth is linked to the growth of the host cambium. This interface between the host tissues and the mistletoe tissues inside the host branch is called the haustorium. The haustorial structures that penetrate the host tissue are called primary and secondary sinkers, which allow them to tap into the host's water and nutrients.

Some mistletoes, particularly the large forms, are primarily parasites of the host's xylem, which moves water and minerals from roots to shoots. Other forms, like the dwarf mistletoes, primarily tap into the host's phloem, which moves sugar and amino acids around the plant. The haustoria of *Viscum album*, a particularly well-studied xylem parasite, do not actually invade the host xylem, but rather the mistletoe vessels and the host vessels anastomose directly in the haustorium. Although it was once thought that primarily xylem-tapping species largely obtain water and minerals only,

Figure 1. Mistletoes.
Left, oak mistletoe (*Phoradenron villosum*) growing on a tree near Berkeley, California. Right, a close-up of the fruits of the desert mistletoe *Phoradendron californicum*.

Phoradendron mistletoes obtain much of their carbon not from the glucose they make through photosynthesis, but by using the recycled sugar that is found in the host's xylem. In *P. californicum*, the desert mistletoe, my collaborators and I found the relative amount of mistletoe-derived versus host-derived carbohydrate found in the mistletoe changed according to the seasons, which in turn influenced the amount of light reaching the mistletoes and how much water was being taken up by the host plant.

How do mistletoes end up growing above the ground on branches of their host plants? Ripe mistletoe fruits are important food for birds and mammals. A sticky, cellulosic substance called 'viscin' that has strong adhesive properties surrounds the strange, evolutionarily derived 'seed' (an embryo that doesn't have a seed coat!). When the animal ingests the seeds, the viscin remains and allows the seed to survive the trip through the frugivore's digestive tract. When the animal regurgitates or defecates the seed, if the seed is lucky, it will land on a stem. The seed will then germinate and immediately its radicle will connect to and then burrow through the host bark and into the stem as described above. If it is a host plant species that the mistletoe can infect, then a haustorium will grow, allowing the mistletoe to tap into the host xylem or phloem. Mistletoes have co-evolved with animals to produce flowers and fruits that signal their presence to pollinators and fruit dispersers with their bright colors.

A consequence of being sessile is that mistletoes on the same host plant individuals may compete with neighboring mistletoes for host resources. Indeed, we found that when single mistletoes are removed experimentally up- or down-'stream' of one another on the host branch, those closer to the source of the flow of water and nutrients have an advantage over those farther away.

What roles do mistletoes play in ecosystems? Abundant research, particularly from Australia, has shown that mistletoes are keystone species. When experimentally removed from hosts locally, the biodiversity of the forest drops. The most dramatic effects are seen on bird diversity. Mistletoe flowers produce nectar and pollen for pollinators, and the female plants produce prolific numbers of fruits, which are in turn used as food by frugivores. Mistletoes are evergreen and used by birds as habitat to build concealed nests. Some mistletoes are host to herbivorous insects like lycaenid butterfly caterpillars. The leaf litter below mistletoes adds important nutrients to the soil and strongly increases the associated arthropod diversity in the leaf litter. The fitness reduction to the host exacted by mistletoes probably also helps maintain higher overall plant diversity locally in these forests by reducing competitive dominance. Finally, mistletoes can also affect the microclimates under their host trees by providing shade — in Australia, when mistletoes are removed, air temperatures increase dramatically, which in turn affects where kangaroos choose to congregate.

Mistletoes can also of course be highly detrimental to host plant growth, survival, and reproduction, and can have a major impact on forestry. However, their negative impact depends on many factors, including the abiotic conditions (e.g., rainfall), the number of mistletoes on the host plant, their size, etc. Paradoxically, often the largest trees in an area are parasitized by the most individual mistletoes. This could be due to the behavior of the bird vectors, for example. In the desert mistletoe system the silky flycatcher *Phainopepla nitens* is the primary seed vector of the parasite, and the adult male birds set up territories they defend in part by perching from the tallest tree around. As they feed on mistletoe berries, they defecate up on these larger trees while defending territories, which then in turn often have large mistletoe infections. A similar pattern is found in Pacific mistletoe (*Phoradendron villosum*), which is a parasite of deciduous California oaks.

How do they overcome host defenses? It is still poorly understood how mistletoes and hosts interact at the molecular level. However, plants have robust physical, chemical, and innate immune defenses in general, and so it is clear that resistance to attack by mistletoes should also evolve. Unlike some parasitic plants, mistletoes don't attack herbaceous plants — they attack woody shrubs and trees. So, *Arabidopsis thaliana* and other genetic model herbaceous plants cannot be used as hosts. Instead, researchers will need to turn to emerging genetic model tree species as hosts to begin to tackle this question.

In response to parasitism by mistletoes, host trees alter production of approximately 25% of their metabolic constituents. The concentrations of some primary metabolites like amino acids are increased and those of some secondary metabolites like phenolics are decreased. This alteration of host metabolism in response to parasitism by mistletoes benefits the parasite at the expense of the host.

Where can I find out more?

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Quick guide

Acacia ants

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What are acacia ants? Acacia ants are a group of specialized defensive symbionts that live in association with trees formerly in the genus *Acacia* (now reclassified as the genus *Vachellia*) and are members of a broader class of 'plant ants' that form mutualistic associations with plants in tropical and sub-tropical regions around the globe. Within ant–acacia symbioses, the acacia trees provide a place for the ants to live and raise their brood, in the form of localized hollow swellings (called 'domatia') of their spines. The trees also offer the ants food, in the form of carbohydrate-rich nectar produced by specialized glands called extra-floral nectaries, and in some cases in Central America, protein-rich packets of food called 'Beltian bodies' produced at the tips of the tree's leaflets. In exchange for these goods, acacia ants protect the trees from a variety of plant enemies. Similar mutualistic associations between acacia ants and acacia trees evolved independently on two continents, Africa (Figure 1) and Central America (Figure 2).

What do acacia ants protect their host trees from? The ants act as 'bodyguards' for their host trees, protecting acacias from herbivores, pathogens, and even encroaching vegetation. Acacia ants regularly patrol their host trees, attacking intruding herbivores when they encounter them. The herbivores can be as tiny as small leaf-feeding insects, or as large as the browsing mammals that roam the African savannas. While acacia ants respond to herbivores' physical presence and odor cues, they can also respond to the unnatural vibrations caused by large mammals feeding on their host trees. For example, African acacia ants dramatically increase their patrolling movements and release volatile alarm pheromones to recruit nestmates when their acacia trees are disturbed by browsers, yet they do not react when the tree is disturbed by an inanimate force such as wind.

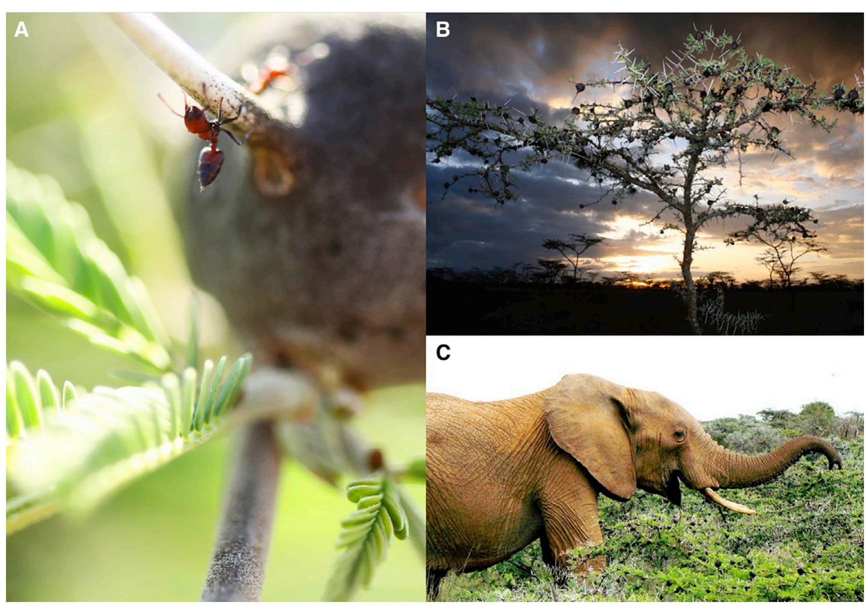

Figure 1. African acacia–ant symbiosis. (A) A *Crematogaster mimosae* acacia ant patrols a spine of the host tree *Acacia* (*Vachellia*) *drepanolobium*. Photo: Todd Palmer. (B) The ant acacia tree *Acacia* (*Vachellia*) *drepanolobium*, showing the hollow swellings in stipular spines that house the acacia ants. Photo: Robert Pringle. (C) An elephant sniffs the canopy of the acacia tree *Acacia* (*Vachellia*) *drepanolobium*; the acacia ants produce pungent "alarm pheromones", which elephants may cue on to determine whether trees are vigorously defended. Photo: Kathleen Rudolph.