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Myrmecophily: The Interaction Networks and Colony Behavior with Ants

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Abstract

The positive interspecies associations between ants and a variety of other organisms (such as plants, other arthropods, and fungi) is called as myrmecophily. A myrmecophile is an organism that lives in association with ants. Myrmecophiles may occupy a variety of ecological niches within their host ant colony. Some consume waste materials in the nests, such as dead ants, dead larvae, or fungi growing in the nest. A few feed on external secretions of ants and some are fed directly by their host ants. Some myrmecophiles feed on the stored food supplies of ants, and a few are predatory on ant eggs, larvae, pupae or even adults. Others benefit the ants by providing a food source for them. Many myrmecophilous relationships are obligate, meaning one or the other participant requires the relationship for survival. Some associations are facultative, benefiting one or both participants but not being necessary to their survival. Many myrmecophiles await discovery and for many the nature of the relationship with their host is unknown.

Keywords: Lycaenidae, Formicidae, Trophobiosis, Mutualism, Speciation

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Introduction:

Myrmecophily is the term applied to positive interspecies associations between ants and a variety of other organisms such as plants, other arthropods, and fungi. Myrmecophily refers to mutualistic associations with ants, though in its more general use the term may also refer to commensal or even parasitic interactions.

The term *myrmecophile* is used mainly for animals that associate with ants. There are an estimated 10,000 species of ants (Formicidae), with a higher diversity in the tropics.[1] In most terrestrial ecosystems ants are ecologically and numerically dominant, being the main invertebrate predators. As a result, ants play a key role in controlling arthropod richness, abundance, and community structure.[2] There is evidence that the evolution of myrmecophilous interactions has contributed to the abundance and ecological success of ants,[1][3] by ensuring a dependable and energy-rich food supply and thus providing a competitive advantage for ants over other invertebrate predators.[4] Most myrmecophilous associations are opportunistic, unspecialized, and facultative (meaning both species are capable of surviving without the interaction), though obligate mutualisms (those in which one or both species are dependent on the interaction for survival) have also been observed for many species.[5]

A myrmecophile is an organism that lives in association with ants. Myrmecophiles may have various roles in their host ant colony. Many consume waste materials in the nests, such as dead ants, dead larvae, or fungi growing in the nest. Some myrmecophiles, however, feed on the stored food supplies of ants, and a few are predatory on ant eggs, larvae, or pupae. Others benefit the ants by providing a food source for them. Most associations are facultative, benefiting one or both participants but not being necessary to their survival, but many myrmecophilous relationships are obligate, meaning one or the other participant requires the relationship for survival.

Myrmecophilous associations are best known in butterflies of the family Lycaenidae. Many lycaenid caterpillars produce nectar by specialized organs and communicate with the ants through sound and vibrations.[6] The association with ants is believed to reduce the parasitisation of the butterfly caterpillars.[7]

There are myrmecophilous beetles in the families Coccinellidae (e.g. the ladybird *Thalassa saginata*), Aphodiidae, Scarabaeidae, Lucanidae, Cholevidae, Pselaphidae, Staphylinidae, Histeridae and Ptiliidae (some treated here as subfamilies). In ant-beetle associations, the myrmecophilous Staphylinids are the most diverse of the beetle families.[8] Myrmecophilous associations are also seen in various other insects such as aphids and treehoppers, as well as the hoverfly genus *Microdon* and several other groups of flies.[9]

Some mites and spiders are also myrmecophilous, particularly some oribatid mites, which have been found to be obligate myrmecophiles.[10][11]

Other myrmecophile groups include

- Orthoptera, like the cricket *Myrmecophilus acervorum*
- Diptera, like the stratiomyid fly *Clitellaria obtusa*
- Molluscs, like *Allopeas myrmekophilos*[12]

The first major work in cataloguing British myrmecophiles was done by Horace Donisthorpe in his 1927 book *The Guests of British Ants*.

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Ant-plant interactions

Ant-plant interactions are geographically widespread,[13] with hundreds of species of myrmecophytic plants in several families including the Leguminosae, Euphorbiaceae, and Orchidaceae.[3] In general, myrmecophytes (or ant plants) usually provide some form of shelter and food in exchange for ant "tending," which may include protection, seed dispersal (see myrmecochory), reduced competition from other plants, hygienic services, and/or nutrient supplementation.[1][14]

Three of the most common and important structural adaptations of ant plants are extrafloral nectaries, domatia, and (least commonly) Beltian bodies. Plant domatia are pre-formed nesting sites provided by the plant in the form of hollow stems, petioles, thorns, or curled leaves.[14] The production of ant-specialized domatia has been documented in over 100 genera of tropical plants.[14] Beltian bodies provide a high-energy food source to ants in the form of nutritive corpuscles produced on leaflet tips,[1] and they have been described in at least 20 plant families.[14] Extrafloral nectaries (EFN's) are known to occur in at least 66 families of angiosperm plants in both temperate and tropical regions, as well as some ferns, but are absent in all gymnosperms and are most abundant in the tropics.[14] EFN's being outside of the plant flowers are not employed in pollination; their primary purpose is to attract and sustain tending ants. Many plants can control the flow of nectar from the EFN's so that the availability of nectar varies according to daily and seasonal cycles. Because ants can respond quickly to changes in flow rate from EFN's, this may be possible mechanism by which plants can induce greater ant activity during times of peak herbivory and minimize overall costs of nectar production.[14] The combined nutritional output of EFN's and Beltian bodies can be a significant food source for tending ants, and in some cases can provide the total nutritive needs for an ant colony.

In exchange for nesting sites and food resources, ants protect plants from herbivores. One the best-known examples of ant-plant mutualism is in bullhorn acacias (*Acacia cornigera*) and their tending *Pseudomyrmex* ants in Central America.[3][13] This system was studied by Dan Janzen in the late 1960s, who provided some of the first experimental evidence that ants significantly reduce herbivory rates of myrmecophytes.[15][16] Since then many other studies have demonstrated similar results in other systems.[3][14] In the Bullhorn acacia system, in exchange for protection the acacias provide domatia, Beltian bodies, and EFN's, and there is evidence that the *Pseudomyrmex* ants can survive exclusively on these food resources without having to forage elsewhere.[1] For many plants, including the bullhorn acacias, ants can significantly reduce herbivory from both phytophagous insects as well as larger organisms, such as large grazing mammals.[17] Obligately associated ant species are some of most aggressive ants in the world, and can defend a plant against herbivory by large mammals by repeatedly biting their attacker and spraying formic acid into the wound.[3]

Myrmecophily is considered a form of indirect plant defense against herbivory, though ants often provide other services in addition to protection. Some ants provide hygienic services to keep leaf surfaces clean and deter disease, and defense against fungal pathogens has also been demonstrated.[14] It is common for ants to prune epiphytes, vines, and parasitic plants from their host plant, and they sometimes thin the shoots of neighboring plants as well. In doing so, ants reduce plant-plant competition for space, light, nutrients, and water.[1] Finally, current work focusing on ants' role in nutrient supplementation for plants has shown that in many ant-plant relationships nutrient flow is bidirectional. One study has estimated that while 80% of the carbon in the bodies of *Azteca* spp. workers is supplied by the host tree (*Cecropia* spp.), 90% of the *Cecropia* tree's nitrogen was supplied by ant debris carried to the tree as a result of external

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foraging.[18] In light of these services, myrmecophily has been consdiered advantageous in ensuring a plant's survival and ecological success,[14] although the costs to the plant of providing for the ants can sufficiently high to offsets benefits.[19]



Fig.1: Mountain Alcon Blue, Phengaris rebeli (L).

Mountain Alcon Blue, Phengaris rebeli (L).

Phengaris rebeli (formerly *Maculinea rebeli*), common name mountain Alcon blue, is a species of butterfly in the family Lycaenidae. It was first found and described in Styria, Austria, on Mount Hochschwab around 1700.[31] Although it was initially classified as a subspecies of *P. alcon*, a European researcher, Lucien A. Berger, designated it as a separate species in 1946. Genetic similarities between *P. rebeli* and *P. alcon* have led many researchers to argue that the two are the same species and differences are due to intraspecific variation.[31]

Although *P. rebeli* is found across the Palearctic (see subspecies), it is difficult to determine the species' precise range due to confusion with *P. alcon*.[32]

Behavioral ecologists have found its role as a brood parasite to be of particular interest as, unlike many brood parasites, it does not directly oviposit in the hosts' nests. *P. rebeli* parasitizes the colony ant species *Myrmica schencki* as a larva by using chemical mimicry to trick the ants into believing that they are ant larvae; thus, the ants bring *P. rebeli* caterpillars back to their nests and feed them.[33] *P. rebeli* is dependent on the plant *Gentiana cruciata* early in its life cycle[34] and is vulnerable to parasitism by *Ichneumon eumerus* while inside the nest of *M. schencki*.[35] It was placed on the IUCN Red List in 2000 and is classified as a species vulnerable to extinction.

Native to temperate grasslands of Central Europe, the Mountain Alcon Blue has silvery blue which are stippled in little black spots with delicate white edges. The butterfly flits harmlessly about in gentle meadows, finds a mate, and then the female lays her eggs on a pretty gentian flower.

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Fig.2: Caterpillar larva of Mountain blue, *Phengaris rebeli* (L), with slave ant.

When the Mountain Alcon blue larva hatches, it eats the gentian until it reaches a certain size whereupon it falls to the ground and releases an allomone—a deceptive chemical which makes it seem identical to an ant larva. Foraging ants discover the caterpillar and tenderly carry it deep within the protection of the ant hive to the nursery room where the ant larvae are fed and cared for. Then the caterpillar reveals another dark talent: it produces a sound which perfectly mimics the ant queen. Subject to this all-powerful voice of authority, the ants care for the caterpillar as though it were the queen–even going so far as to attack the actual queen. Obeying the dictates of the awful song, the ants feed the still living ant larvae to the caterpillar which devours the helpless young ants like so many little wiggling burritos (well, if juvenile butterflies ate burritos). When the butterfly pupates into an adult, it loses its ability to mimic ant chemicals or produce the queen's voice. The ants recognize it as an invader and attack, but the butterfly's scales are designed to resist their mandibles. It flees the crippled and abused ant colony and begins the cycle over again. Yet monsters still must fear other monsters and there is an even more invidious predator which seeks out the Alcon larvae deep within ant hives. This is the parasitic wasp, Ichneumon eumerus, which infiltrates ant colonies which are being preyed on by Phengaris rebeli larvae. The wasp locates the caterpillar and then releases an allomone which causes the ants to go insane and attack one another. Then in the chaos that follows, the wasp injects its eggs into the living caterpillar. When the eggs hatch they eat the interloper from inside and then burst out of its carcass.

Ant-insect interactions

Ants tend a wide variety of insect species, most notably lycaenid butterfly caterpillars and hemipterans.[5] Forty-one percent of all ant genera include species that associate with insects.[20] In all ant-insect associations the ants provide some service in exchange for nutrients in the form of honeydew, a sugary fluid excreted by many phytophagous insects.[5] Interactions between honeydew-producing insects and ants is often called trophobiosis, a term which merges notions of trophic relationships with symbioses between ants and insects. This term has been criticized, however, on the basis that myrmecophilous

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interactions are often more complex than simple trophic interactions, and the use of symbiosis is inappropriate for describing interactions among free-living organisms.[5]

Hemiptera

Some of the most well-studied myrmecophilous interactions involve ants and hemipterans (earlier grouped in the order Homoptera which included the Auchenorrhyncha and Sternorrhyncha), especially aphids. There are around 4000 described species of aphids, and they are the most abundant myrmecophilous organisms in the northern temperate zones.[3][5] Aphids feed on the phloem sap of plants, and as they feed they excrete honeydew droplets from their anus. The tending ants ingest these honeydew droplets then return to their nest to regurgitate the fluid for their nestmates (see trophallaxis).[1] Between 90-95% of the dry weight of aphid honeydew is various sugars, while the remaining matter includes vitamins, minerals, and amino acids.[3] Aphid honeydew can provide an abundant food source for ants (aphids in the genus *Tuberolachnus* can secrete more honeydew droplets per hour than their body weight) and for some ants aphids may be their only source of food. In these circumstances, ants may supplement their honeydew intake by preying on the aphids once the aphid populations have reached certain densities. In this way ants can gain extra protein and ensure efficient resource extraction by maintaining honeydew flow rates that do not exceed the ants' collection capabilities.[3] Even with some predation by ants, aphid colonies can reach larger densities with tending ants than colonies without. Ants have been observed to tend large "herds" of aphids, protecting them from predators and parasitoids. Aphid species that are associated with ants often have reduced structural and behavioral defense mechanisms, and are less able to defend themselves from attack than aphid species that are not associated with ants.[3]

Ants engage in associations with other honeydew-producing hemipterans such as scale insects (Coccidae), mealybugs (Pseudococcidae), and treehoppers (Membracidae), and most of these interaction are facultative and opportunistic with some cases of obligate associations, such as hemipterans that are inquiline, meaning they can only survive inside ant nests.[5] In addition to protection, ants may provide other services in exchange for hemipteran honeydew. Some ants bring hemipteran larvae into the ant nests and rear them along with their own ant brood.[3] Additionally, ants may actively aid in hemipteran dispersal: queen ants have been observed transporting aphids during their dispersive flights to establish a new colony, and worker ants will often carry aphids to a new nesting site if the previous ant nest has been disturbed. Ants may also carry hemipterans to different parts of a plant or to different plants in order to ensure a fresh food source and/or adequate protection for the herd.

Lycaenid butterflies

Myrmecophily among lycaenid caterpillars differs from the associations of hemipterans because caterpillars feed on plant tissues, not phloem sap, and therefore do not continually excrete honeydew. Caterpillars of lycaenid butterflies have therefore evolved specialized organs that secrete chemicals to feed and appease ants.[3] The secretions are a mixture of sugar and amino acid which in synergy is more attractive to the ants than either component in its own.[21] Because caterpillars do not automatically pass honeydew, they must be stimulated to secrete droplets and do so in response to ant antennation, which is the drumming or stroking of the caterpillar's body by the ants' antennae.[2] Some caterpillars possess specialized receptors that allow them to distinguish between ant antennation and contact from predators

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and parasites, and others produce acoustic signals that agitate ants, making them more active and likely better defenders of the larvae.[22][23] As with homopteran myrmecophiles, ants protect Lycaenid larvae from predatory insects (including other ants) and parasitoid wasps, which lay their eggs in the bodies of many species of Lepidoptera larvae. For example, one study conducted by Pierce and colleagues in Colorado experimentally found that for the larvae of *Glaucopsyche lygdamus* that were tended by a certain ant species (*Formica podzolica*), compared to untended larvae, the percentage of larvae disappearing from plants before late final instar decreased (not statistically significantly, though) and the percentage of larvae infected by parasitoids significantly decreased (from 33% to 9%–12%).[24] These interactions do not come without an energetic cost to the butterfly, however, and it has been shown that ant-tended individuals reach smaller adult sizes than non-tended individuals due to the costs of appeasing ants during the larval stage.[25] Interactions with ants are not limited to the butterfly's larval stage, and in fact ants can be important partners for butterflies at all stages of their life cycle.[2] For example, adult females of many lycaenid butterflies, such as *J. evagoras*[26], preferentially oviposit on plants where ant partners are present, possibly by using ants' own chemical cues in order to locate sites where juvenile butterflies will likely be tended by ants.[23] Finally, while ant attendance has been most widely documented in Lycaenid butterflies and to some extent in riodinid butterflies such as *E. elvina*[27], many other lepidopteran species are known to associate with ants, including many moths.[23]

Rove beetles

Multiple levels of myrmecophily

Many trophobiotic ants can simultaneously maintain associations with multiple species.[20] Ants that interact with myrmecophilous insects and myrmecophytes are highly associated: species that are adapted to interact with one of these myrmecophiles may switch among them depending on resource availability and quality. Of the ant genera that include species that associate with ant plants, 94% also include species that associate with trophobionts. In contrast, ants that are adapted to cultivate fungus (leaf cutter ants, tribe Attini) do not possess the morphological or behavioral adaptations to switch to trophobiotic partners.[20] Many ant mutualists can exploit these multi-species interactions to maximize the benefits of myrmecophily. For example, some plants will host aphids instead of investing in EFN's, which may be more energetically costly depending on local food availability.[5] The presence of multiple interactors can strongly influence the outcomes of myrmecophily, often in unexpected ways.[28]

Significance of myrmecophily in ecology

Mutualisms are geographically ubiquitous, found in all organismic kingdoms, and play a major role in all ecosystems.[28][29] Combined with the fact that ants are one of the most dominant lifeforms on earth,[13] it is clear that myrmecophily plays a significant role in the evolution and ecology of diverse organisms, and in the community structure of many terrestrial ecosystems.

Evolution of positive interactions

Questions of how and why species coevolve are of great interest and significance. In many myrmecophilous organisms it is clear that ant associations have been influential in the ecological success, diversity, and persistence of species. Analyses of phylogenetic information for myrmecophilous

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organisms as well as ant lineages have demonstrated that myrmecophily has arisen independently in most groups multiple times. Because there have been multiple gains (and perhaps losses) of myrmecophilous adaptations, the evolutionary sequence of events in most lineages is unknown.[25] Exactly how these associations evolve also remains unclear.

In studying the coevolution of myrmecophilous organisms, many researchers have addressed the relative costs and benefits of mutualistic interactions, which can vary drastically according to local species composition and abundance, variation in nutrient requirements and availability, host plant quality, presence of alternative food sources, abundance and composition of predator and parasitoid species, and abiotic conditions.[20] Because of the large amounts of variation in some of these factors, the mechanisms that support the stable persistence of myrmecophily are still unknown.[28] In many cases, variation in external factors can result in interactions that shift along a continuum of mutualism, commensalism, and even parasitism. In almost all mutualisms, the relative costs and benefits of interactions are asymmetrical; that is, one partner experiences greater benefits and/or fewer costs than the other partner. This asymmetry leads to "cheating," in which one partner evolves strategies to receive benefits without providing services in return. As with many other mutualisms, cheating has evolved in interactions between ants and their partners. For example, some lycaenid larvae are taken into ant nests where they prey on ant brood and offer no services to the ants.[3] Other lycaenids may parasitize ant-plant relationships by feeding on plants that are tended by ants, apparently immune to ant attack because of their own appeasing secretions. Hemipterophagous lycaenids engage in a similar form of parasitism in ant-hemipteran associations.[14] In light of the variability in outcomes of mutualistic interactions, and also the evolution of cheating in many systems, much remains to be learned about the mechanisms that maintain mutualism as an evolutionarily stable interaction.[29]

Species coexistence

In addition to leading to coevolution, mutualisms also play an important role in structuring communities.[28] One of the most obvious ways in which myrmecophily influences community structure is by allowing for the coexistence of species which might otherwise be antagonists or competitors. For many myrmecophiles, engaging in ant associations is first and foremost a method of avoiding predation by ants. For example, the caterpillars of lycaenid butterflies are an ideal source of food for ants: they are slow-moving, soft-bodied, and highly nutritious, yet they have evolved complex structures to not only appease ant aggression but to elicit protective services from the ants.[2] In order to explain why ants cooperate with other species as opposed to preying on them, two related hypotheses have been proposed: cooperation either provides ants with resources that are otherwise difficult to find, or it ensures the long-term availability of those resources.[5]

Community structure

At both small and large spatiotemporal scales, mutualistic interactions influence patterns of species richness, distribution, and abundance.[30] Myrmecophilous interactions play an important role in determining community structure by influencing inter- and intraspecific competition; regulating population densities of arthropods, fungi, and plants; determining arthropod species assemblages; and influencing trophic dynamics.[5] Recent work in tropical forests has shown that ant mutualisms may play

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key roles in structuring food webs, as ants can control entire communities of arthropods in forest canopies.[14] Myrmecophily has also been key in the ecological success of ants. Ant biomass and abundance in many ecosystems exceeds that of their potential prey, suggesting a strong role of myrmecophily in supporting larger populations of ants than would otherwise be possible.[14] Furthermore, by providing associational refugia and habitat amelioration for many species, ants are considered dominant ecosystem engineers.[3][30]

Myrmecophily as a model system

Myrmecophilous interactions provide an important model system for exploring ecological and evolutionary questions regarding coevolution, plant defense theory, food web structure, species coexistence, and evolutionarily stable strategies. Because many myrmecophilous relationships are easily manipulable and tractable, they allow for testing and experimentation that may not be possible in other interactions. Therefore, they provide ideal model systems in which to explore the magnitude, dynamics, and frequency of mutualism in nature.[14]

Conclusion

It is possible to unveil several aspects of the biology of one of the least-known groups of myrmecophilous butterflies. This includes variation in host-plant use and degree of myrmecophily, an unrecorded morphological variation during ontogeny in ant-related traits, a novel type of larval ant-organ, and a new interpretation for the mechanism whereby larvae of *Theope* can manipulate the behaviour of their tending ants. As new avenues of research, the understanding of how the different ecological syndromes have evolved in *Theope* is a priority, but this can only be attained with a robust phylogenetic hypothesis for the genus, and with additional information on the life histories of other species in Theopeina. As *Theope* is the most diverse genus of myrmecophilous riodinids, with many new species having been described in recent years, it is expected that there are many other yet unknown ways to be a myrmecophile in this fascinating group of butterflies.

References

1. B. Holldobler and E.O. Wilson, The Ants, Cambridge, Massachusetts: The Belknap Press of Harvard University Press, 1990.
2. K. Fiedler, B. Holldobler, and P. Seufert, "Butterflies and ants: The communicative domain," Cellular and molecular life sciences, vol. 52, 1996, pp. 14-24.
3. B. Holldobler and E.O. Wilson, Journey to the Ants, Cambridge, Massachusetts: The Belknap Press of Harvard University Press, 1994.
4. N. Bluthgen, N.E. Stork, and K. Fiedler, "Bottom-up control and co-occurrence in complex communities: honeydew and nectar determine a rainforest ant mosaic," Oikos, vol. 106, 2004, pp. 344-358.
5. B. Stadler and T. Dixon, Mutualism: Ants and their insect partners, Cambridge: Cambridge University Press, 2008.

Received:25 June 2018/Accepted:11 September 2018/Published:20 December 2018

6. Pierce NE, Braby MF, Heath A, Lohman DJ, Mathew J, Rand DB, Travassos MA. 2002. The ecology and evolution of ant association in the Lycaenidae (Lepidoptera.) ANNUAL REVIEW OF ENTOMOLOGY 47: 733-771.
7. H. T. Baumgarten & K. Fiedler (1998). "Parasitoids of lycaenid butterfly caterpillars: different patterns in resource use and their impact on the hosts' symbiosis with ants". Zoologischer Anzeiger. 236: 167–180.
8. Lapeva-Gjonova, Albena (April 2013). "Ant-Associated Beetle Fauna in Bulgaria: A Review and New Data". Psyche (Cairo: Hindawi Pub. Co.) 2013: 1-14
I. Brake (1999). "Prosaetomilichia de Meijere: a junior subjective synonym of Milichia Meigen, with a phylogenetic review of the myrmecophila species-group [Diptera, Milichiidae]". Tijdschrift voor Entomologie. 142 (1): 31–36.
9. Paula E. Cushing (1997). "Myrmecomorphy and myrmecophily in spiders: A review". Florida Entomologist: 165–193.
10. F. Ito & G. Takaku (1994). "Obligate myrmecophily in an oribatid mite. Novel symbiont of ants in the Oriental tropics". Naturwissenschaften. 81 (4): 180–182. doi:10.1007/BF01134538.
11. V. Witte; R. Janssen; A. Eppenstein; U. Maschwitz (2002). "Allopeas myrmekophilos (Gastropoda, Pulmonata), the first myrmecophilous mollusc living in colonies of the ponerine army ant Leptogenys distinguenda (Formicidae, Ponerinae)". Insectes Sociaux. 49 (4): 301–305. doi:10.1007/PL00012646.
12. V. Rico-Gray and P. Oliveira, The Ecology and Evolution of Ant-Plant Interactions, Chicago and London: University of Chicago Press, 2007.
13. M. Heil and D. McKey, "Protective ant-plant interactions as model systems in ecological and evolutionary research," Annual Review of Ecology, Evolution, and Systematics, vol. 34, 2003, pp. 425-453.
14. D. Janzen, "Coevolution of mutualism between ants and acacias in Central America," Evolution, vol. 20, 1966, pp. 249-275.
15. D. Janzen, "Interaction of the bull's-horn acacia (Acacia cornigera L.) with an ant inhabitant (Pseudomyrmex ferruginea F. Smith) in Eastern Mexico," Univ. Kansas Sci. Bull. , vol. 47, 1967, pp. 315-558.
16. Stanton, M. L. and T. M. Palmer (2011). "The high cost of mutualism: effects of four species of East African ant symbionts on their myrmecophyte host tree". Ecology. 92: 1073–1082.
17. G. Alvarez, I. Armbrecht, E. Jimenez, H. Armbrecht, and P. Ulloa-Chacon, "Ant-plant Association in Two Tococa Species From a Primary Rain Forest of Colombian Choco (Hymenoptera: Formicidae)," Sociobiology, vol. 38, 2001, pp. 558-602.
18. Stanton, M. L. and T. M. Palmer (2011). "The high cost of mutualism: effects of four species of East African ant symbionts on their myrmecophyte host tree". Ecology. 92: 1073–1082.
19. T.H. Oliver, S.R. Leather, and J.M. Cook, "Macroevolutionary patterns in the origin of mutualisms involving ants," Journal of Evolutionary Biology, vol. 21, Nov. 2008, pp. 1597-1608.
20. Wada, Ayako; Isobe, Yu; Yamaguchi, Susumu; Yamaoka, Ryohei; Ozaki, Mamiko (2001-10-01). "Taste-enhancing Effects of Glycine on the Sweetness of Glucosea Gustatory Aspect of Symbiosis between the Ant, Camponotus japonicus, and the Larvae of the Lycaenid Butterfly,

Received:25 June 2018/Accepted:11 September 2018/Published:20 December 2018

Niphanda fusca". Chemical Senses. 26 (8): 983–992. doi:10.1093/chemse/26.8.983. ISSN 0379-864X.

21. A.A. Agrawal and J.A. Fordyce, "Induced indirect defence in a lycaenid-ant association: the regulation of a resource in a mutualism ," Proceedings of the Royal Society of London, vol. 267, 2000, pp. 1857-1861.
22. K. Fiedler, Systematic, evolutionary, and ecological implication of myrmecophily within the Lycaenidae, UND Museum Alexander Koenig: Bonner Zoologische Monographien, 1991.
23. A.M. Fraser, A.H. Axen, and N.E. Pierce, "Assessing the Quality of Different Ant Species as Partners of a Myrmecophilous Butterfly," Oecologia, vol. 129, Nov. 2001, pp. 452-460.
24. N.E. Pierce, M.F. Braby, A. Heath, D.J. Lohman, J. Mathew, D.B. Rand, and M.A. Travassos, "The ecology and evolution of ant association in the Lycaenidae (Lepidoptera)," Annual Review of Entomology, vol. 47, 2002, pp. 733-771.
25. Biology of Australian butterflies. Kitching, R. L. (Roger Laurence), 1945-, CSIRO (Australia). Collingwood, VIC, Australia: CSIRO Pub. 1999. ISBN 0643050272. OCLC 40792921.
26. Horvitz, Carol C.; Turnbull, Christine; Harvey, Donald J. (1987-07-01). "Biology of Immature Eurybia elvina (Lepidoptera: Riodinidae), a Myrmecophilous Metalmark Butterfly". Annals of the Entomological Society of America. 80 (4): 513–519. doi:10.1093/aesa/80.4.513. ISSN 0013-8746.
27. J. Hoeksema and E. Bruna, "Pursuing the big questions about interspecific mutualism: a review of theoretical approaches," Oecologia, vol. 125, 2000, pp. 321-330.
28. M. Doebeli and N. Knowlton, "The evolution of interspecific mutualisms," Proceedings of the National Academy of Sciences of the United States of America, vol. 95, 1998, pp. 8676-8680.
29. J.J. Stachowicz, "Mutualism, Facilitation, and the Structure of Ecological Communities," BioScience, vol. 51, Mar. 2001, pp. 235-246.
30. Maculinea rebeli". UniProt Consortium. Retrieved 2009-02-09.
31. Steiner, F; , Schlick-Steiner B.C. , Hçttinger H. , Nikiforov A. , Moder K. and Christian E. (2006). "Maculinea alcon and M. rebeli (Insecta: Lepidoptera: Lycaenidae) – one or two alcon blues? Larval cuticular compounds and egg morphology of East Austrian populations". Ann. Naturhist. Mus. Wien. 107B: 165–180. JSTOR 41767345.
32. Steiner, F.M; B.C . Schlick-Steiner , H . Höttinger 1 , A . Nikiforov , K . Moder & E . Christian (2006). "Geographical versus food plant differentiation in populations of Maculinea alcon (Lepidoptera: Lycaenidae) in Northern Hungary" (PDF). Ann. Naturhist. Mus. Wien. 107B: 165–180. Retrieved 23 October 2013.
33. Akino, T; JJ Knapp; JA Thomas; GW Elmes (1999). "Chemical mimicry and host specificity in the butterfly Maculinea rebeli, a social parasite of Myrmica ant colonies". Proceedings of the Royal Society B. 266 (1427): 1419–1426. doi:10.1098/rspb.1999.0796. PMC 1690087. Retrieved 28 September 2013.
34. Kéry, M; Matthies, D & Fischer, M (2001). "The effect of plant population size on the interactions between the rare plant Gentiana cruciata and its specialized herbivore Maculinea rebeli". Journal of Ecology. 89 (3): 418–427. doi:10.1046/j.1365-2745.2001.00550.x. Retrieved 19 October 2013.

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35. Hochberg, M; Elmes, G. W.; Thomas, J. A.; Clarke, R. T (1996). "Mechanisms of local persistence in coupled host-parasitoid associations: the case model of Maculinea rebeli and Ichneumon eumerus". Philosophical Transactions: Biological Sciences. 351 (1348): 1713–1724. Bibcode:1996RSPTB.351.1713H. doi:10.1098/rstb.1996.0153. Retrieved 19 October 2013.
36. https://ferrebeekeeper.wordpress.com/tag/alcon-blue/

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