Behavioral, ecological and evolutionary mechanisms underlying caterpillar-ant symbioses

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At least 30 different groups in seventeen butterfly and moth families (Lepidoptera) include ant-associated caterpillars. The life histories of more than 900 ant-associated species have been documented from the butterfly families Lycaenidae and Riodinidae, with relationships ranging from parasitism to mutualism. Caterpillars that appear to secrete food rewards for ants are not necessarily mutualists, and a number of species are known to manipulate ants with deceptive chemical and vibratory signals. The functional variability of different exocrine glands deployed as 'ant organs' makes them prone to convergence, and it remains unclear whether ant association originated more than once in lycaenids and riodinids. The relative costs and benefits of caterpillar integration with ants is context dependent: both top-down and bottom-up effects influence the evolution of ant associations.

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Introduction

A diverse group of specialized organisms associate with ants, including many species of moths and butterflies that not only coexist with ants, but actively seek out ant-dominated habitat spaces [1••]. More than 300 Neotropical butterfly species in the families Hesperiidae, Papilionidae, and Nymphalidae have been documented at *Eciton burchellii* army ant swarm raids, where they find and consume nitrogen-rich bird droppings. Many of these species are specifically attracted by *Eciton* activity and have therefore been called 'antbutterflies' [2]. Most other lepidopteran-ant associations revolve around the caterpillar stage, taking advantage of enemy-free space or food resources provided by ants. In these species, caterpillars attract ants or ovipositing adults seek out areas where ants

are present [3•,4••,5]. Caterpillar-ant associations appear to have arisen at least thirty times across butterflies and moths in seventeen families (Figure 1) [3•]. Different aspects of the behavioral ecology of ant-associated caterpillars have been reviewed in depth by Casacci *et al.* [4••] and Pierce and Dankowicz [3•] in the last two years, following the last major review 20 years ago [6]. In this mini-review, we highlight important recent developments and outstanding questions in understanding the diversity and evolution of ant-associated caterpillars.

The most significant recent contributions to understanding ant-caterpillar associations lie in two areas: first, robust phylogenies of Lepidoptera [e.g. Ref. 7] now provide the foundation to investigate numerous aspects of life history evolution in these groups. Second, extensive work has uncovered the previously undescribed life histories of individual species in key groups, especially for lycaenid butterflies in the Afrotropics and lycaenid/riodinid butterflies in Central/South America. These accounts have filled in many gaps in our understanding of broad evolutionary trends.

These contributions have also enabled identification of another area where data are missing. Well-designed sampling efforts are needed to detect and understand the evolution and abundance of ant-associated caterpillars, particularly those in the tropics living on ant plants [e.g. Ref. 8] or on trees routinely occupied by canopy-dwelling ants such as *Crematogaster* and *Oecophylla* species [e.g. Ref. 9]. Many ant associations have been difficult to detect because caterpillars rely on ant territoriality and hygiene to drive away enemies, but rarely approach or interact directly with ants themselves. For example, *Homodes* caterpillars (Erebidae) are morphological mimics of *Oecophylla smaragdina* workers, and caterpillars exclusively inhabit trees dominated by these highly aggressive ants [3•]. This form of obligate ant dependency can only be detected by careful surveys of the insects feeding on plants both inside and outside the territories of different ants. Similarly, detritivorous caterpillars have been reared from refuse deposits of *Eciton* army ants in Panama but were never described [2], and the literature is replete with other moth caterpillars found in ant nests but never identified [3•].

We focus here on Lycaenidae and Riodinidae, the only two lepidopteran families where larval ant associations have been described in depth for dozens of species [3•] (Table 1). These families are sister groups [7], and

Figure 1
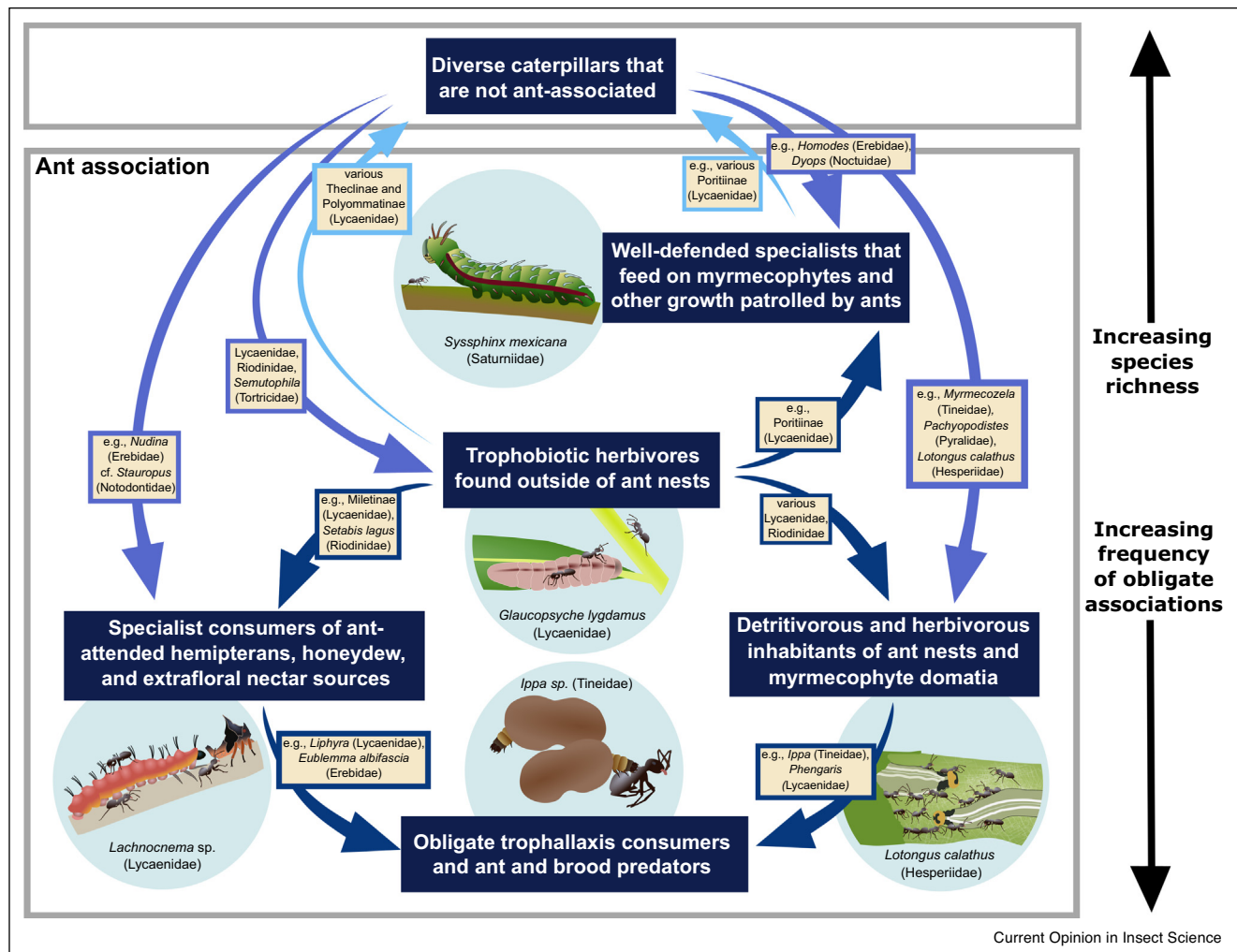
Different forms of caterpillar-ant association in the Lepidoptera illustrated with possible examples. At least 30 different groups in seventeen families of butterflies and moths have ant-associated caterpillars. The natural history and evolution of ant-associated caterpillars is described in more detail in Ref. [3•], though only brief mention is given to the extraordinary mutualism of *Lotongus calathus* (Hesperiidae, illustrated bottom right). Caterpillars of this species weave large communal shelters by rolling leaflets on rattan palms [5]. Hundreds of *Dolichoderus* ants colonize each shelter and reinforce the original silk structure using caterpillars' frass [67]. Females of *L. calathus* lay eggs only in the presence of the ants and often oviposit on existing ant-inhabited shelters. As a result, a single shelter can be continuously occupied by several overlapping generations of caterpillars. Defended by ants, *L. calathus* can reach exceptional densities, making them an occasional pest of commercially grown palms [5].

assuming that closely related taxa in the same genus share similar life histories, we can extrapolate from well-documented cases that at least 70% of the ~5000 species of Lycaenidae and 20% of the ~1500 species of Riodinidae associate with ants [3•]. These numbers include both obligate associates that require ants to complete their life cycles, and facultative ones that do not strictly require ants to survive. Lycaenid and riodinid species span the gamut from mutualist partners to parasites and predators of ants (Figure 1), and this variation sets them apart from other ant-associated animal groups. What most ant-associated species have in common is that caterpillars produce reward substances, substrate vibrations, or chemical signals to attract and manipulate ants to serve as bodyguards

[3•]. A smaller fraction of species in these families do not actively interact with ants, but seem to have behavioral, chemical, or morphological defenses that protect immature stages from attack by ants, enabling them to feed or shelter in the 'enemy free space' found within or close to ant nests [e.g. Ref. 10].

Origin and variability of 'ant organs'

Espeland *et al.* [7] concluded that ant associations arose convergently in Lycaenidae, Eurybiini, and Nymphidiini, but as part of their analysis, scored Dianesiini and Stalachtini (Riodinidae) as non-ant-associated. However, immature stages of Dianesiini have never been described and could be ant-associated, and caterpillars of Stalachtini

Table 1

Numbers of species with documented ant associations, simplified from Ref. [3•]. The life histories of less than 15% of lycaenid and riodinid species are sufficiently well documented to designate their caterpillars as ant-associated or confidently rule out the possibility of ant association, but these percentages are much greater if we extrapolate our results to their closest relatives (at least 70% of the ~5000 species of Lycaenidae and 20% of the ~1500 species of Riodinidae [3•]). Of the ant-associated taxa, larval relationships of 183 lycaenids and 43 riodinids cannot yet be classified as either obligate or facultative.

Butterflies	Total ant associates	Obligate ant associates	Butterflies	Total ant associates	Obligate ant associates
LYCAENIDAE	881	344	RIODINIDAE	68	22
Curetinae	5	0	Nemeobiinae	0	0
Poriitinae	71	63	Eurybiini	7	3
Aphnaeinae	122	115	Nymphidiini	61	19
Miletinae	51	32		0	0
Lycaeninae	10	0	Dianesiini, Calydnini, Symmachiini, Emesidini, Riodinini, and Helicopini		
Theclinae + Polyommatinae	622	134			

possess 'nectary' tentacle organs and are sometimes ant-attended (Figure 2). Given the recent placement of Calydnini within the sister group of ant-associated Nymphidiini [11], it's possible that future ancestral state reconstructions will find that ant association originated in the common ancestor of Lycaenidae and Riodinidae.

Lycaenid and riodinid diversification is a story of extensive convergence and functional variability in organs used for defense, mutualism, and manipulation of ants. Caterpillars in both families possess several discrete organs that seem to elicit and maintain ant associations, including a few that occur in almost all lycaenids or riodinids:

Figure 2

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Camponotus cf. *blandus* workers attracted to an aggregation of *Stalachtis phlegia* (Riodinidae) caterpillars in Ponta Negra, Natal, Rio Grande do Norte, Brazil, on December 8, 2013. Caterpillars on the top left and bottom of the group have everted yellow 'nectary' tentacle organs as indicated. Photo by Lucas Kaminski.

Pore Cupola Organs (PCOs) are single-celled cuticular glands whose exact function remains unknown, although they appear to play an important signaling role in gaining favorable recognition by ants. PCOs have been found in all riodinid and lycaenid larvae that have been examined, whether or not they are ant-associated, although the density of PCOs often correlates with the degree of interest that ants show not only in a given species of caterpillar, but also in particular regions, such as the thorax or seventh abdominal segment [3•,4••]. Comparative study of PCO secretion and deployment could provide important clues regarding the origins and basic underlying features of ant association.

Tentacle Organs (TOs) are paired, eversible structures that are always found on the eighth abdominal segment and exhibit considerable functional variability in terms of variation across species [12•]. They are widely distributed across lycaenids and riodinids (Figure 3). Non-ant-associated riodinids like *Mesosemia* (Eurybiini) secrete visible droplets from the TOs to defend against predators and parasitoids [13,14]. 'Nectary' TOs of ant-associated Eurybiina and most Nymphidiini (Riodinidae) produce similar droplets that are instead nutritious and imbibed by ants. In many Nymphidiini with normal 'nectary' TOs, thoracic 'anterior tentacle organs' allow caterpillars to excite attendant ants at will, and these may represent TOs that have been developmentally modified [15]. In a handful of carnivorous and parasitic Nymphidiini, the abdominal TOs release only volatile chemicals to manipulate ants [12•,16••].

Most lycaenids have a **Dorsal Nectary Organ** (DNO) on the seventh abdominal segment that performs an analogous reward function to the 'nectary' TOs of riodinids, freeing the tentacle organs to perform other tasks (Figure 3) [15]. Lycaenid TOs appear to release volatile chemicals, although secretions have been difficult to collect and characterize. In most lycaenids they ostensibly produce 'alarm' signals to excite ant bodyguards, but the

Figure 3
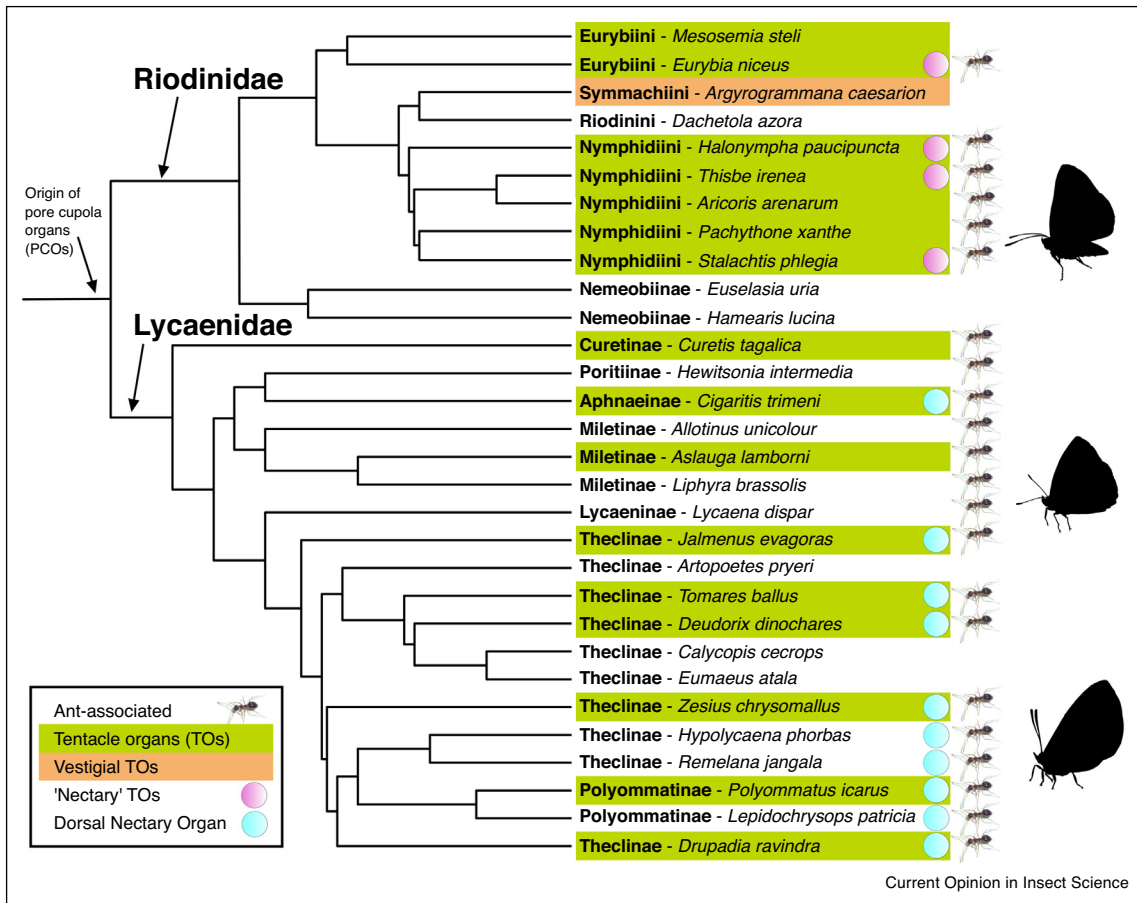
Exemplars of caterpillar morphologies across the phylogeny of Lycaenidae and Riodinidae to indicate the presence/absence of ant-associated exocrine glands as well as ant association. The exemplars were chosen to represent all known losses of TOs, 'nectary' TOs, and ant association for riodinids, and all known losses of TOs and DNOs for lycaenids in the subfamilies Curetinae, Miletinae, Poritiinae, and Lycaeninae. Within the remaining Lycaenidae, TOs and the DNO have been lost in dozens of additional clades within Aphnaeinae, Theclinae, and Polyommatinae (not represented), and ant association has similarly been lost in additional clades of Poritiinae, Lycaeninae, Theclinae, and Polyommatinae (not represented). Phylogeny based on analyses of Ref. [11] for Riodinidae, [7] for Lycaenidae, and [18] for Miletinae, with character mapping based on Refs. [3•,16••,19,20]. Phylogeny drawn with the help of Ref. [21]. Butterfly silhouettes by Christopher Adams.

enormous tentacle organs of *Curetis* are a special case. In the absence of ants, *Curetis* TOs may dispel diverse threats including spiders and wasps [3•]. MicroCT scans recently documented the musculature and tissue structure underlying 'ant organs' in parasitic *Cigaritis lilacinus*; comparable detail generally remains unavailable for other lycaenids or riodinids [17].

Evolution of caterpillar interactions and integration with ants

Parasitic and mutualistic caterpillar-ant interactions are difficult to discriminate. The sugar-rich food droplets produced by trophobiotic hemipterans and caterpillars of *Semutophila* (Tortricidae) and consumed by attendant ants are a form of excrement that is produced continuously whether ants are present to consume it or not. However, the sweet droplets of lycaenids and riodinids are not a waste product but are exudates from specialized

exocrine glands that are under considerable caterpillar control. Although they are attractive to ants, these exudates may not provide ants with net positive benefits [22].

Costs and benefits of ant rewards are context dependent. Secretions from the specialized glands of lycaenids and riodinids like the Australian species *Jalmenus evagoras* can be beneficial to ants in some contexts, but exert a fitness cost on attendant ants in others, when ants care for lycaenid caterpillars at the expense of their own brood [26]. *Arhopala japonica* (Theclinae) superficially appears to be facultatively mutualistic, but this species is now known to produce drug-like secretions that are ingested by ants, directly altering their brain chemistry and making ants into aggressive bodyguards with reduced locomotory ability [25]. Deceptive communication is another tactic caterpillars use to manipulate ant behavior: various lycaenid species mimic chemical and vibratory signals

produced by host ants and their mutualists [4••,23,24]. When ants cannot discriminate between other ants, true mutualists, and lycaenid caterpillars, they lack an effective option to prevent caterpillars from stealing ants' attention and resources. Overall, a complex and largely unknown array of drug-like substances and deceptive signals seems to give lycaenids the upper hand in their relationships with ants.

Basic questions about interactions with ants remain unanswered even for the best-studied lycaenids, such as species in the Palearctic genus *Phengaris* (Polyommatinae). For example, although long suspected, a report confirming the existence in *Phengaris alcon (='rebeli')* of a fixed polymorphism of caterpillars requiring either one year or two years of larval growth in the host ant nest has only recently been published [27]. Strikingly, the late instar caterpillars of this genus feed directly on ant brood or like 'cuckoos' via regurgitations (trophallaxis) within nests of *Myrmica* ants, and yet may still produce copious' reward' secretions for ants like their 'mutualistic' relatives, and in some cases use these as part of adoption rituals [28,29]. It seems likely that these secretions contain compounds that manipulate the behavior and fidelity of attendant ants, as in certain lycaenid and aphid species [25,30]. In this respect, it would be valuable to know more, too, about the secretions of larvae of the African genus *Lepidochrysops* (Polyommatinae), the only other group of caterpillars known to be phyto-predaceous, with early instar larvae feeding on flowers before switching to direct carnivory or trophallaxis, but only in the nests of formicine ants. A description was recently published of competitive exclusion between *Phengaris* caterpillars and a fungus that parasitizes their host ants [31].

Few studies have systematically compared DNO secretions across a range of species, and TO and PCO secretions are essentially unknown, though several recent studies have examined cuticular hydrocarbons (CHCs) of larval Theclinae, Polyommatinae, and Lycaeninae. CHCs communicate ant status and colony membership, and they similarly determine caterpillars' reception among ants [4••,9,32–34]. For example, cuticular alkenes can trigger ant aggression toward caterpillars and are correspondingly absent in lycaenids [32]. Lycaenid CHCs typically appear to help caterpillars avoid attack; many lycaenids have camouflaging CHC profiles that blend in with their host plants [35•,36]. Inui *et al.* [37] studied three *Arhopala* species in Borneo that feed only on *Macaranga* host-plants heavily defended by ant symbionts. Each caterpillar species employs a different strategy through its CHC profile to evade ant defenses. *Arhopala zylda*, which possesses few CHCs shared with ants and may lack chemical signatures detectable by the ants, does not secrete reward substances and is ignored by nearby ants [10,37]. The other two species attract ants normally to drink the secretions at their DNO. *Arhopala amphimuta*

has its own idiosyncratic CHC profile that may prove to chemically mimic its host plant, and *A. dajagaka* has a CHC profile much like that of its attending ants that allows it to be recognized as a nestmate [34,37]. It seems plausible that in some cases, a signal from the DNO secretions can also function as a communication signal, so different species may exhibit trade-offs in the deployment of different chemical strategies to attract and maintain ant bodyguards. Cuticular hydrocarbon mimicry plays a critical role in the complex host associations of *Phengaris* caterpillars, social parasites that specialize on different *Myrmica* ant species at the level of individual butterfly populations [4••,38,39•,40]. CHCs not only help parasitic caterpillars like *Phengaris* and *Niphanda* survive in their host colony, but may encourage ants to carry them inside the nest through mimicry of ant brood CHC profiles [34]. On a similar note, Di Salvo *et al.* [41] proposed that *Serratia* bacteria shared by phytophagous and later-stage *P. alcon* caterpillars and their host ants might produce pheromones that help caterpillars integrate with their hosts. Microbial relationships may be quite intricate— the *P. alcon* gut microbiome has also been shown to change when larvae move into ant nests and switch from plant-feeding to a trophallaxis diet [41,42].

The lycaenid subfamilies Miletinae, Aphnaeinae, and Poritiinae form a clade largely restricted to the Afrotropical and Oriental regions [7]. These three subfamilies provide an interesting case study because of the extreme variation in their ant interactions. The Miletinae are predators that feed on ant-attended hemipterans, and while caterpillars are often attractive to ants, they do not produce reward secretions [18]. Most Aphnaeinae, in contrast, are phytophagous and eagerly attended by ants for their reward substances [43]. Meanwhile, ants appear to be indifferent or repelled by poritiine larvae, which are covered with long bristles. Nonetheless, immature stages of many species of Poritiinae in the African tribe Liptenini have only been documented to occur close to ant nests and foraging trails, where caterpillars feed on lichens [3•,44].

Despite differences in their larval ecology, these three groups share certain behaviors that underly their ant associations. Ovipositing females and caterpillars of most Miletinae, Aphnaeinae, and Poritiinae are strongly attracted to ants, and ant pheromones likely serve as important oviposition cues [18,44–46]. Moreover, adult Miletinae and Poritiinae frequently interact with ants while feeding on honeydew and extrafloral nectaries in the tree canopy [3•,46–48]. Except for species with facultative ant associations in the genera *Feniseca*, *Spalgis*, and *Taraka* (Miletinae), all Miletinae and Aphnaeinae are obligate ant associates never found far from ants [3•]. Correspondingly, the genus or subfamily of associated ant is strongly conserved across Miletinae and Aphnaeinae [18,43]. A considerable number of Poritiinae are not obligate ant associates, but obligate relationships with

ants are likely to have been important in the evolution of the relatively large African tribe within this group, the Liptenini [3•].

Lycaenid and riodinid phylogenies suggest numerous transitions between potentially mutualistic, parasitic, and more or less commensal relationships with ants. Obligate behaviors to shelter in ant nests, thus qualifying caterpillars as 'myrmecophiles' in the strictest sense [1••], appear convergently dozens of times [3•]. More than twenty lycaenid and riodinid groups—at least half of them in the lycaenid subfamilies Aphnaeinae and Miletinae—have independently evolved entomomophagous diets based on ant brood, trophallaxis, or both [3•,18,43].

The chemical basis of integration with ants is largely unknown in riodinids, but life history convergences with lycaenids suggest that similar mechanisms of interaction must be involved. Most riodinids are plant-feeding and secrete reward substances to attract ant bodyguards, but some are carnivorous. Kaminski *et al.* [16••] recently described the first 'cuckoo' riodinid caterpillar, *Aricoris arenarum* (Nymphidiini). While early instars feed on hemipteran honeydew, later instars of this species rely on trophallaxis from ants to feed within the nest, as in the Palearctic species *Niphanda fusca* (Lycaenidae: Polyommatinae) [3•,16••].

Four other carnivorous riodinid lineages have been recognized in the Eurybiini and Nymphidiini, of which the largest is the subtribe Pachythonina (Nymphidiini) [12•,49]. Immature stages of Pachythonina were unknown until recently, and it now appears possible that all 30+ species will prove carnivorous, either feeding on hemipterans or ant brood [11,12•]. As specialist associates of notoriously aggressive ants including species of *Azteca* and *Pseudomyrmex*, larvae of Pachythonina are heavily armored and closely resemble some Miletinae (Lycaenidae) [9,12•,50,51]. In the Lycaenidae, the best-armored caterpillars belong to *Liphyra* spp. (Miletinae), whose tank-like larvae prey on brood of green tree ants, *O. smaragdina*, in Australia, New Guinea, and Southeast Asia. The integument of these larvae looks like chain-link armor, and is composed of densely packed, modified setae that protect the caterpillar against ant attack while allowing it to be flexible enough to walk with a hydrostatic skeleton [52]. This unique arrangement was the only known example of its kind in Lepidoptera, until a similarly shielded caterpillar of *Pseudonymphidia agave* (Riodinidae: Pachythonina) was discovered among brood of the aggressive predatory ant *Neoponera villosa* in Mexico [50].

Assuming that ant associations were present ancestrally, they have been lost at least twice in Riodinidae and in countless groups of Lycaenidae (Figure 3). For many species, mortality is many-fold higher in the absence of attending ants. However, some predators and parasitoids use ants to find their caterpillar prey [53]. For facultative ant associates, parasitism rates that increase with caterpillar density may discourage overly intense ant associations and ultimately lead to their dissolution [e.g. Ref. 54].

Climate, nutrients, and ant communities

Obligate ant associates are mostly extreme specialists that either live inside ant nests or are associated with ant species like *Crematogaster* and *Camponotus* that form large, ecologically dominant, long-lived colonies [55•]. Facultative ant associates are mostly flexible in forming associations with different ant species, although some do considerably better with certain ant species than others [56]. Some species of Theclinae and Polyommatinae casually associate with more than a dozen ant genera [55•]. These and related facultative ant associates are well-served by some invasive ant species [55•,57] and integrate readily with native ant communities when introduced to new areas [58]. Because of this flexibility, facultative ant associates usually have larger ranges and habitat tolerances. Although there may be hundreds of obligate ant associates found across a given region, the species found at any given site tend to be overwhelmingly facultative. Lycaenidae are concentrated in the Old World tropics and subtropics, while Riodinidae are concentrated in the New World tropics and subtropics. Lycaenid and riodinid clades that have spread beyond these foci of diversity into temperate and outlying areas are all either facultative ant associates or non-ant associates [3•,59].

Despite the preponderance of research on top-down predation and parasitism of ant-associated caterpillars, a variety of bottom-up effects are likely to have important local effects on their diversity. In general, lowered environmental concentrations of nitrogen and other nutrients may dramatically change the economics of ant behavior and ant-symbiont interactions. In Australia, nutrient-poor soils give rise to a surplus of available carbohydrate-rich nectar and honeydew sources that may increase the overall abundance of ants and stabilize ant dominance hierarchies. Moreover, nitrogen-fixing plants are dominant and may attract both ants and caterpillars [6,60]. The resulting stability of Australian ant communities is favorable to obligate ant associates, and this is likely why the diversity of caterpillar-ant associations in Australia is rivaled only in tropical forests [3•]. Trophobiotic caterpillars may also find it metabolically easier to attract ants in Australia, as Australian honeydew and nectar sources generally have unusually low nitrogen concentrations [60]. In the same ways, nutrient limitations may help explain why obligate trophobiotic ant associations as well as myrmecochorous plants are unusually common in Southern Africa [3•,60]. Rising atmospheric CO_2 levels can similarly increase C:N ratios in plant tissues, and resulting effects on caterpillar metabolism and ant food sources may encourage or break down different aspects of ant-caterpillar interactions depending on the species of

caterpillar, ant, and host plant, as documented in analogous studies for various ant-associated aphids [61].

Sodium, (Na) phosphorus (P) and and calcium (K) availability, as well as the stoichiometry of different other nutrients and micronutrients can have a critical influences over ant behavior and community structure, and are likely to affect ant symbionts as well [62[••],63]. The availability of Na matters because unlike plants, animals require Na for metabolism since they osmoregulate using Na-K pumps. They must also replenish Na since it is constantly being excreted. Soils poor in sodium and phosphorus such as those found in Australia and Southern Africa can create situations where Na and P are limiting nutrients for plant consumers and decomposers. Provided caterpillars of Lycaenidae can concentrate and secrete Na and P, it is plausible that limitation of these key micronutrients may have facilitated the evolution of the relatively large number of obligately associated species of Lycaenidae that occur in these habitats [62[••]]. The only specific molecules that have been identified and quantified from lycaenid and riodinid DNO secretions are sugars and amino acids [4[••],23], although the presence of other, unknown substances seems likely [e.g. Ref. 25]. Intriguingly, sucrose or trehalose paired with the amino acid glycine was significantly more attractive to host ants than either component alone, and the synergy of this kind of 'umami' effect may be important in accounting for the extreme attractiveness of lycaenid secretions to attendant ants [64]. A systematic survey of secretions across species and habitats would contribute significantly to our understanding of caterpillar-ant associations.

Conclusions

The life histories of butterflies are arguably better known than those of any other invertebrate group, and yet only a small fraction have been fully documented for Lycaenidae and Riodinidae (let alone for moths). Citizen science platforms like iNaturalist are a growing source of information for conservation and comparative biology [65,66], and a recent iNaturalist project to collect butterfly ant interactions already has over 500 observations (https://www.inaturalist.org/projects/ant-butterfly-interactions-borboletas-formigueiras). This information, combined with the wealth of phylogenies being published for both Lycaenidae and Riodinidae, may enable study of the convergence they exhibit in multiple life history traits associated with ant symbioses, thereby gaining insights into the processes underlying these associations as well as the evolutionary patterns that they create.

Conflict of interest statement

Nothing declared.

Acknowledgements

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- •• of outstanding interest

1. Parker J, Kronauer DJC: **How ants shape biodiversity**. *Curr Biol*
•• 2021, **31**:R1208-R1214 http://dx.doi.org/10.1016/j.cub.2021.08.015
This article introduces the rise of ants, their tremendous impact on shaping terrestrial biodiversity by eliminating many ecological niches and creating others, and the effects of human disturbances on ant-dominated ecosystems.

2. Pérez-Espona S: *Eciton* **army ants—umbrella species for conservation in Neotropical forests**. *Diversity* 2021, **13**:136 http://dx.doi.org/10.3390/d13030136.

3. Pierce NE, Dankowicz E: **The natural history of ant-caterpillar**
• **associations**. In *Caterpillars in the Middle*. Edited by Marquis RJ, Koptur S. Springer; 2022
This review tabulates and provides species counts for the different known groups of ant-associated Lepidoptera. Natural history, behavior, and ecology of each group are described.

4. Casacci LP, Bonelli S, Balletto E, Barbero F: **Multimodal signaling**
•• **in myrmecophilous butterflies**. *Front Ecol Evol* 2019, **7**:454 http://dx.doi.org/10.3389/fevo.2019.00454
In this paper, the authors review different signals produced by lycaenids to manipulate ants, and the cues used by lycaenids to 'eavesdrop' on ants, including recent insights on *Phengaris* social parasites.

5. Steiner H: *The Insect Fauna of Rattan. A Study of Potential Pest Species on* **Calamus manan** *and Other Rattan Palms in Peninsula Malaysia*. 2001 . Digitized at Deutsche Gesellschaft Technische Zusammenarbeitwww.yumpu.com/s/mmqfZYuDAiES7hcn.

6. Pierce NE, Braby MF, Heath A, Lohman DJ, Mathew J, Rand DB, Travassos MA: **The ecology and evolution of ant association in the Lycaenidae (Lepidoptera)**. *Ann Rev Entomol* 2002, **47**:733-771.

7. Espeland M, Breinholt J, Willmott KR, Warren AD, Vila R, Toussaint EF, Maunsell SC, Aduse-Poku K, Talavera G, Eastwood R *et al.*: **A comprehensive and dated phylogenomic analysis of butterflies**. *Curr Biol* 2018, **28**:770-778 http://dx.doi.org/10.1016/j.cub.2018.01.061.

8. Baker CC, Bittleston LS, Sanders JG, Pierce NE: **Dissecting host-associated communities with DNA barcodes**. *Philos Trans R Soc B Biol Sci* 2016, **371** http://dx.doi.org/10.1098/rstb.2015.0328 2015.0328.

9. Dejean A, Azémar F, Libert M, Compin A, Herault B, Orivel J, Bouyer T, Corbara B: **Ant-lepidopteran associations along African forest edges**. *Sci Nat* 2016, **104**:7 http://dx.doi.org/10.1007/s00114-016-1424-6.

10. Shimizu-kaya U, Okubo T, Yago M, Inui Y, Itioka T: **Myrmecoxeny in *Arhopala zylda* (Lepidoptera, Lycaenidae) larvae feeding on *Macaranga myrmecophytes***. *Entomol News* 2013, **123**:63-70 http://dx.doi.org/10.3157/021.123.0115.

11. Seraphim N, Kaminski LA, Devries PJ, Penz C, Callaghan C, Wahlberg N, Silva-Brandao KL, Freitas AV: **Molecular phylogeny and higher systematics of the metalmark butterflies (Lepidoptera: Riodinidae)**. *Syst Entomol* 2018, **43**:407-425 http://dx.doi.org/10.1111/syen.12282.

12. Mota LL, Kaminski LA, Freitas AV: **The tortoise caterpillar:**
• **carnivory and armoured larval morphology of the metalmark butterfly *Pachythone xanthe* (Lepidoptera: Riodinidae)**. *J Nat*

Hist 2020, **54**:309-319 http://dx.doi.org/10.1080/00222933.2020.1759720

This is the first study to describe the full life history of a member of the carnivorous riodinid subtribe Pachythonina, spotlighting convergence with miletine lycaenid butterflies.

13. Nielsen GJ, Kaminski LA: **Immature stages of the Rubiaceae-feeding metalmark butterflies (Lepidoptera: Riodinidae), and a new function for the tentacle nectary organs**. *Zootaxa* 2018, **4524**:1-32 http://dx.doi.org/10.11646/zootaxa.4524.1.1.

14. Nielsen GJ, Kaminski LA: **Subtle life cycle differences between two sympatric *Mesosemia* (Lepidoptera: Riodinidae) butterflies**. *Stud Neotrop Fauna Environ* 2021:1-10 http://dx.doi.org/10.1080/01650521.2021.1895511.

15. Campbell DL, Pierce NE: **Phylogenetic relationships of the Riodinidae: implications for the evolution of ant association**. *Butterflies: Ecology and Evolution Taking Flight*. University of Chicago; 2003:395-408.

16. Kaminski LA, Volkmann L, Callaghan CJ, DeVries PJ, Vila R: **The**
•• **first known riodinid 'cuckoo' butterfly reveals deep-time convergence and parallelism in ant social parasites**. *Zool J Linn Soc* 2020:1-20 http://dx.doi.org/10.1093/zoolinnean/zlaa150

This paper describes the first full life history of a riodinid that parasitizes host ants within their nest feeding on regurgitations (trophallaxis), spotlighting convergence of riodinids with many parasitic and carnivorous lycaenids.

17. Basu DN, Kunte K: **Tools of the trade: MicroCT reveals native structure and functional morphology of organs that drive caterpillar–ant interactions**. *Sci Rep* 2020, **10**:1-7 http://dx.doi.org/10.1038/s41598-020-67486-5.

18. Kaliszewska ZA, Lohman DJ, Sommer K, Adelson G, Rand DB, Mathew J, Talavera G, Pierce NE: **When caterpillars attack: biogeography and life history evolution of the Miletinae (Lepidoptera: Lycaenidae)**. *Evolution* 2015, **69**:571-588 http://dx.doi.org/10.1111/evo.12599.

19. Kaminski LA, Mota LL, Freitas AV: **Larval cryptic coloration and mistletoe use in the metalmark butterfly Dachetola azora (Lepidoptera: Riodinidae)**. *Entomol Am* 2014, **120**:18-23 http://dx.doi.org/10.1664/13-RA-008R.1.

20. Fiedler K: **Systematic, evolutionary, and ecological implications of myrmecophily within the Lycaenidae (Insecta: Lepidoptera: Papilionoidea)**. *Bonn Zool Monogr* 1991, **31**:1-210.

21. Letunic I, Bork P: **Interactive Tree Of Life (iTOL) v5: an online tool for phylogenetic tree display and annotation**. *Nucleic Acids Res* 2021, **49**:W293-296 http://dx.doi.org/10.1093/nar/gkab301.

22. Fiedler K, Hölldobler B, Seufert P: **Butterflies and ants: the communicative domain**. *Experientia* 1996, **52**:14-24.

23. Daniels H, Gottsberger G, Fiedler K: **Nutrient composition of larval nectar secretions from three species of myrmecophilous butterflies**. *J Chem Ecol* 2005, **31**:2805-2821 http://dx.doi.org/10.1007/s10886-005-8395-y.

24. Lin YH, Liao YC, Yang CC, Billen J, Yang MM, Hsu YF: **Vibrational communication between a myrmecophilous butterfly *Spindasis lohita* (Lepidoptera: Lycaenidae) and its host ant *Crematogaster rogenhoferi* (Hymenoptera: Formicidae)**. *Sci Rep* 2019, **9**:1-10 http://dx.doi.org/10.1038/s41598-019-54966-6.

25. Hojo MK, Pierce NE, Tsuji K: **Lycaenid caterpillar secretions manipulate attendant ant behavior**. *Curr Biol* 2015, **25**:2260-2264 http://dx.doi.org/10.1016/j.cub.2015.07.016.

26. Pierce NE, Nash DR: **The imperial blue, *Jalmenus evagoras* (Lycaenidae)**. *Monographs on Australian Lepidoptera* 1999, **vol 6**277-313.

27. Elmes GW, Wardlaw JC, Schönrogge K, Thomas JA: **Evidence of a fixed polymorphism of one-year and two-year larval growth in the myrmecophilous butterfly *Maculinea rebeli***. *Insect Conserv Divers* 2019, **12**:501-510.

28. Fiedler K: **New information on the biology of *Maculinea nausithous* and *M. teleius* (Lepidoptera: Lycaenidae)**. *Nota Lepidopterol* 1990, **12**:246-256.

29. Wardlaw JC, Thomas JA, Elmes GW: **Do *Maculinea rebeli* caterpillars provide vestigial mutualistic benefits to ants when living as social parasites inside *Myrmica* ant nests?** *Entomol Exp Appl* 2000, **95**:97-103 http://dx.doi.org/10.1046/j.1570-7458.2000.00646.x.

30. Kudo T, Aonuma H, Hasegawa E: **A symbiotic aphid selfishly manipulates attending ants via dopamine in honeydew**. *Sci Rep* 2021, **11**:1-8.

31. Tartally A, Szabó N, Somogyi AÁ, Báthori F, Haelewaters D, Mucsi A, Fürjes-Mikó Á, Nash DR: **Ectoparasitic fungi of *Myrmica* ants alter the success of parasitic butterflies**. *Sci Rep* 2021, **11** http://dx.doi.org/10.1038/s41598-021-02800-3.

32. Morozumi Y, Murakami T, Watanabe M, Ohta S, Ômura H: **Absence of cuticular alkenes allows lycaenid larvae to avoid predation by *Formica japonica* ants**. *Entomol Sci* 2019, **22**:126-136 http://dx.doi.org/10.1111/ens.12342.

33. Sprenger PP, Menzel F: **Cuticular hydrocarbons in ants (Hymenoptera: Formicidae) and other insects: how and why they differ among individuals, colonies, and species**. *Myrmecol News* 2020, **30**:1-26 http://dx.doi.org/10.25849/myrmecol.news_030:013.

34. Barbero F: **Cuticular lipids as a cross-talk among ants, plants and butterflies**. *Int J Mol Sci* 2016, **17**:1966 http://dx.doi.org/10.3390/ijms17121966.

35. Lima LD, Trigo JR, Kaminski LA: **Chemical convergence**
• **between a guild of facultative myrmecophilous caterpillars and host plants**. *Ecol Entomol* 2021, **46**:66-75 http://dx.doi.org/10.1111/een.12941

This study is the first to demonstrate a link between caterpillar cuticular hydrocarbons (CHCs) and host plant CHCs for several lycaenid species occurring around ants.

36. Lohman DJ, Liao Q, Pierce NE: **Convergence of chemical mimicry in a guild of aphid predators**. *Ecol Entomol* 2006, **31**:41-51 http://dx.doi.org/10.1111/j.0307-6946.2006.00758.x.

37. Inui Y, Shimizu-kaya U, Okubo T, Yamsaki E, Itioka T: **Various chemical strategies to deceive ants in three *Arhopala* species (Lepidoptera: Lycaenidae) exploiting *Macaranga myrmecophytes***. *PLoS One* 2015, **10**:e0120652 http://dx.doi.org/10.1371/journal.pone.012065.

38. Casacci LP, Schönrogge K, Thomas JA, Balletto E, Bonelli S, Barbero F: **Host specificity pattern and chemical deception in a social parasite of ants**. *Sci Rep* 2019, **9** http://dx.doi.org/10.1038/s41598-018-38172-4 1-0.

39. Tartally A, Thomas JA, Anton C, Balletto E, Barbero F, Bonelli S,
• Bräu M, Casacci LP, Csősz S, Czekes Z, Dolek M: **Patterns of host use by brood parasitic *Maculinea* butterflies across Europe**. *Philos Trans R Soc B* 2019, **374**:20180202 http://dx.doi.org/10.1098/rstb.2018.0202

The authors review the complex host association patterns of *Phengaris* social parasites across Europe, and present evidence that *Phengaris* have coevolved with different hosts across a geographic mosaic, creating resiliency across populations.

40. Tartally A, Somogyi AÁ, Révész T, Nash DR: **Host ant change of a socially parasitic butterfly (*Phengaris alcon*) through host nest take-over**. *Insects* 2020, **11**:556 http://dx.doi.org/10.3390/insects11090556.

41. Di Salvo M, Calcagnile M, Talà A, Tredici SM, Maffei ME, Schönrogge K, Barbero F, Alifano P: **The microbiome of the *Maculinea-Myrmica* host-parasite interaction**. *Sci Rep* 2019, **9**:1-10 http://dx.doi.org/10.1038/s41598-019-44514-7.

42. Szenteczki MA, Pitteloud C, Casacci LP, Kešnerová L, Whitaker MR, Engel P, Vila R, Alvarez N: **Bacterial communities within *Phengaris* (*Maculinea*) alcon caterpillars are shifted following transition from solitary living to social parasitism of *Myrmica* ant colonies**. *Ecol Evol* 2019, **9**:4452-4464 http://dx.doi.org/10.1002/ece3.5010.

43. Boyle JH, Kaliszewska ZA, Espeland M, Suderman TR, Fleming J, Heath A, Pierce NE: **Phylogeny of the Aphnaeinae: myrmecophilous African butterflies with carnivorous and herbivorous life histories**. *Syst Entomol* 2015, **40**:169-182 http://dx.doi.org/10.1111/syen.12098.

44. Sáfián S, Larsen TB: **On the ecology and behavior of *Cerautola crowleyi* (Sharpe, 1890), *Cerautola ceraunia* (Hewitson, 1873) and *Cerautola miranda* (Staudinger, 1889) with descriptions of early stages (Lepidoptera: Lycaenidae, Epitolini)**. *Trop Lepid Res* 2009, **1**:22-28.

45. Heath A: **A review of African genera of the tribe Aphnaeini (Lepidoptera: Lycaenidae)**. *Metamorphosis* **(Suppl. 2)**:1997:1-60.

46. Fiedler K, Maschwitz U: **Adult myrmecophily in butterflies: the role of the ant *Anoplolepis longipes* in the feeding and oviposition behaviour of *Allotinus unicolor* (Lepidoptera, Lycaenidae)**. *Trans Lepid Soc Jpn* 1989, **40**:241-251.

47. Wagner DL, Gagliardi BL: **Hairstreaks (and other insects) feeding at galls, honeydew, extrafloral nectaries, sugar bait, cars, and other routine substrates**. *Am Entomol* 2015, **61**:160-167 http://dx.doi.org/10.1093/ae/tmv045.

48. Van Noort S, Moll E: **Observations on feeding behaviour of adults of the common Buff butterfly, *Baliochila aslanga* (Lycaenidae: Poritiinae) at extra-floral nectaries on *Adenopodia spicata* (Mimosaceae)**. *Metamorphosis* 2019, **30**:25-29.

49. Kaminski LA, Lima LD: **Larval omnivory in the myrmecophilous butterfly *Setabis lagus lagus* (Riodinidae: Nymphidiini)**. *J Lepid Soc* 2019, **73**:276-279 http://dx.doi.org/10.18473/lepi.73i4.a4.

50. Pérez-Lachaud G, Rocha FH, Pozo C, Kaminski LA, Seraphim N, Lachaud JP: **Filling the gap: a new ant-butterfly symbiosis in the forest canopy**. *Sci Rep.* 2021, **11** http://dx.doi.org/10.1038/s41598-021-00274-x 20770.

51. Kaminski LA, Carneiro E, Dolibaina DR, Casagrande MM, Mielke OH: **Oviposition of *Minstrellus grandis* (Lepidoptera: Riodinidae) in a harmful ant-plant symbiosis**. *Acta Amazon* 2020, **50**:256-259 http://dx.doi.org/10.1590/1809-4392202001801.

52. Dupont ST, Zemeitat DS, Lohman DJ, Pierce NE: **The setae of parasitic *Liphyra brassolis* butterfly larvae form a flexible armour for resisting attack by their ant hosts (Lycaenidae: Lepidoptera)**. *Biol J Linn Soc* 2016, **117**:607-619.

53. Elgar MA, Nash DR, Pierce NE: **Eavesdropping on cooperative communication within an ant-butterfly mutualism**. *Sci Nat* 2016, **103**:84 http://dx.doi.org/10.1007/s00114-016-1409-5.

54. Bächtold A, Alves-Silva E, Del-Claro K: **Ant-related oviposition is not associated to low parasitism of the myrmecophilous butterfly *Allosmaitia strophius* in an extrafloral nectaried shrub**. *Acta Oecol* 2017, **83**:15-21.

55. Fiedler K: **The ant associates of Lycaenidae butterfly**
• **caterpillars–revisited**. *Nota Lepidopterol* 2021, **9**:159 http://dx.doi.org/10.3897/nl.44.68993.
The author collected and analyzed published records of the ant hosts and degree of association of caterpillars in the lycaenid subfamilies Aphnaeinae, Theclinae, and Polyommatinae. This is the first published survey of this type in 20 years.

56. Mizuno T, Hagiwara Y, Akino T: **Varied effects of tending ant species on the development of facultatively myrmecophilous lycaenid butterfly larvae**. *Insects* 2019, **10**:234 http://dx.doi.org/10.3390/insects10080234.

57. Ikenaga N, Touyama Y, Kameyama T, Ito F: **Effects of Argentine ants (Hymenoptera: Formicidae) on myrmecophilous lycaenid butterfly, *Narathura bazalus* (Lepidoptera: Lycaenidae), in western Japan**. *Entomol Sci* 2020, **23**:69-73 http://dx.doi.org/10.1111/ens.12396.

58. Dexheimer E, de Araújo HN, Despland E: **Novel mutualistic interaction in introduced *Polyommatus icarus* larvae in Quebec**. *J Entomol Soc Ontario* 2021, **152**:29-38.

59. Patrick B, Patrick H: *Butterflies of the South Pacific*. Otago University Press; 2012.

60. Orians GH, Milewski AV: **Ecology of Australia: the effects of nutrient-poor soils and intense fires**. *Biol Rev* 2007, **82**:393-423 http://dx.doi.org/10.1111/j.1469-185X.2007.00017.x.

61. Blanchard S, Lognay G, Verheggen F, Detrain C: **Today and tomorrow: impact of climate change on aphid biology and potential consequences on their mutualism with ants**. *Physiol Entomol* 2019, **44**:77-86 http://dx.doi.org/10.1111/phen.12275.

62. Kaspari M: **The seventh macronutrient: how sodium shortfall**
•• **ramifies through populations, food webs and ecosystems**. *Ecol Lett* 2020, **23**:1153-1168 http://dx.doi.org/10.1111/ele.13517
The author builds a compelling case for the importance of sodium in modulating plant interactions with herbivores and mutualists, thereby also shaping the geographical distributions of trophobionts and ants.

63. Reihart RW, Angelos KP, Gawkins KM, Hurst SE, Montelongo DC, Laws AN, Pennings SC, Prather CM: **Crazy ants craving calcium: macronutrients and micronutrients can limit and stress an invaded grassland brown food web**. *Ecology* 2020, **102**:e03263 http://dx.doi.org/10.1002/ecy.3263.

64. Hojo MK, Wada-Katsumata A, Ozaki M, Yamaguchi S, Yamaoka R: **Gustatory synergism in ants mediates a species-specific symbiosis with lycaenid butterflies**. *J Comp Physiol A* 2008, **194**:1043-1052.

65. Mesaglio T, Soh A, Kurniawidjaja S, Sexton C: **'First Known Photographs of Living Specimens': the power of iNaturalist for recording rare tropical butterflies**. *J Insect Conserv* 2021, **23**:1-7 http://dx.doi.org/10.1007/s10841-021-00350-7.

66. Sanderson C, Braby MF, Bond S: **Butterflies Australia: a national citizen science database for monitoring changes in the distribution and abundance of Australian butterflies**. *Austral Entomol* 2021, **60**:111-127.

67. Igarashi S, Fukuda H: *The Life Histories of Asian Butterflies*. Tokai University Press; 1997.