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*Review*

# *Eciton* Army Ants—Umbrella Species for Conservation in Neotropical Forests

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**Abstract:** Identification of priority areas for conservation is crucial for the maintenance and protection of biodiversity, particularly in tropical forests where biodiversity continues to be lost at alarming rates. Surveys and research on umbrella species can provide efficient and effective approaches to identify potential areas for conservation at small geographical scales. Army ants of the genus *Eciton* are keystone species in neotropical forests due to their major role as top predators and due to the numerous vertebrate- and invertebrate associated species that depend upon their colonies for survival. These associates range from the iconic army ant-following birds to a wide range of arthropod groups, some of which have evolved intricate morphological, behavioural and/or chemical strategies to conceal their presence and integrate into the colony life. Furthermore, *Eciton* colonies require large forested areas that support a diverse leaf litter prey community and several field-based and genetic studies have demonstrated the negative consequences of forest fragmentation for the long-term maintenance of these colonies. Therefore, *Eciton* species will not only act as umbrella for their associates but also for many other species in neotropical forests, in particular for those that require a large extent of forest. This review summarises past and recent accounts of the main taxonomic groups found associated with *Eciton* colonies, as well research assessing the impact of forest fragmentation on this army ant, to encourage the adoption of *Eciton* army ants as umbrella species for the identification of priority areas for conservation and assessments of the effect of disturbance in neotropical forests.

**Keywords:** antbird; army ant; biodiversity; biological indicator; conservation; deforestation; habitat fragmentation; myrmecophiles; mimicry; species interactions; tropics

## 1. Introduction

Disturbance as a consequence of anthropogenic activities continues to be a major driver of biodiversity loss [1–4] and it negatively impacts ecosystems functioning and ecosystem services [5–7]. In tropical forests, anthropogenically-caused disturbance as a result of logging, land clearance for agriculture and hunting [8,9] are ongoing threats to biodiversity and ecosystem function [10,11]. Therefore, to devise effective conservation actions and sustainable management of tropical forests resources, it is important to determine and predict the effects of anthropogenic disturbance in these biodiversity-rich areas [12,13]. However, the assessment of anthropogenic disturbance on biodiversity in tropical forests is challenging due to the lack of knowledge on a large number of taxa in these areas, including those not yet discovered and described [14], and the limited budgets and timeframes for conducting biodiversity assessments [15]. These challenges have partly been overcome by conducting surveys of a reduced number of well-known and identifiable taxonomic groups (or species) that can act as biological indicators to determine the level or magnitude of anthropogenic disturbance [16–19], although not without caveats [20–23].

Insects represent a large part of the biodiversity found in tropical forests and play a central role in ecosystem function and services [24,25]. Owing to their short life cycles and

habitat disturbance sensitivity, insects are considered suitable biological indicators for monitoring the effects of fragmentation and other environmental changes on biodiversity [26,27] as well as for monitoring the sustainable use of tropical forests [28]. Furthermore, insects are also used as biodiversity indicators, with their diversity used as surrogate information for species richness estimates in a given area or to identify priority areas for conservation [22]. Among insects, ants comprise the largest fraction of animal biomass in the tropics and are frequently used as environmental, ecological and biodiversity indicators [29–33]. In the Neotropics, army ants are dominant components in forests and as top predators of arthropod communities play a major role in leaf litter community structure [34–36]. The most conspicuous army ants in neotropical forests are those within the genus *Eciton*, due to their large hunting raids and the numerous invertebrate and vertebrate species associated with them that exploit the different environments and conditions provided by these ants' colony life [29,36–38]. Furthermore, *Eciton* colonies are particularly sensitive to landscape fragmentation and deforestation, with large areas of continuous forests required for their long-term survival [34,39].

Monitoring of biodiversity and ecosystems function is essential for the maintenance and sustainable use of neotropical forests [28,40]. Biodiversity conservation through area protection or other effective area-based conservation approaches requires the identification of areas of high biodiversity, high irreplaceability, large intact habitats with a high degree ecological integrity and/or high vulnerability due to the impact of anthropogenic activities [12,13]. Surveys assessing the presence and abundance of *Eciton* colonies in a particular area could provide additional information on the selection of conservation areas in neotropical forests. Although *Eciton* army ants have been used as biodiversity or habitat integrity indicators [41], they have not yet been implicitly considered as umbrella species for biodiversity conservation in neotropical forests or considered as biological indicators to assess the impacts of forest disturbance.

This review aims to encourage the adoption of *Eciton* army ants as potential umbrella species for neotropical forest biodiversity conservation. To this end, I build on previous detailed accounts of *Eciton* colony associates [37,38,42] to provide further insights derived from research conducted in the last decade, including the significant contributions of genetic and genomic studies to our understanding on the relationship of some of these associates with their *Eciton* hosts. Furthermore, this review also summarises research on the effect of deforestation or other land-use changes on *Eciton* colonies, to illustrate the potential use of these army ants in applied research assessing the impact of disturbance or success of restoration projects in neotropical forests.

## 2. *Eciton* Army Ants

Several ant genera within the subfamily Dorylinae are referred to as army ants, with the genera *Cheliomyrmex*, *Eciton*, *Labidus*, *Neivamyrmex* and *Nomamyrmex* forming a monophyletic group and found in tropical and subtropical regions in the American continent [43,44]. Army ants are characterised by presenting the "army ant syndrome" which includes the evolution of behavioural and reproductive traits that have allowed them to be key predators in neotropical forests. This suite of traits includes obligate collective foraging, nomadic lifestyle, and highly specialised queens which are characterised by being wingless and having large expanding abdomens capable of lying thousands of eggs [38,45–47]. Colony founding of *Eciton* army ants is by fission. When colonies attain a large size, a sexual brood is produced, containing a small number of new queens and hundreds of males. The parental colony will then divide into two daughter colonies, one of them headed by a new queen and the other one headed either by the old queen or another of the new queens [36,48]. Initial phylogenetic analyses based on data derived from three nuclear genes, one mitochondrial gene, and morphological analyses, suggested that the evolution of the "army ant syndrome" in army ants species in the Americas and Afro-Eurasia was as a result of inheritance of these traits from a unique Gondwanan common ancestor [46]. However, a recent comprehensive phylogenomic study based on 2,166 loci

has indicated multiple origins for the "army ant syndrome" in different continents [44]; therefore, supporting initial views of convergent evolution of this syndrome [38].

The genus is distributed from Mexico to Argentina [38], with 12 *Eciton* species, and several subspecies, described [49]. Genomic analyses using a large number of loci (> 4,000,000) for 146 specimens, collected from a wide distribution range and representing those nine species for which workers and queens are known, strongly supported interspecific relationships congruent with taxonomic classifications [50]. However, further taxonomic revisions are required to delimit species and subspecies boundaries. For example, a phylogeographic study based on mitochondrial DNA sequences indicated that genetic divergence of *E. burchellii foreli* and *E. b. parvispinum* colonies was higher than between other morphologically described species [51].

Foraging and emigration of *Eciton* army ants takes place above ground [36,52]. The species *E. burchellii* and *E. hamatum* are considered truly epigaeic, as they bivouac above ground. Other *Eciton* species such as *E. mexicanum*, *E. vagans* and *E. dulcium* tend to bivouac in more sheltered and darker places, inside or beneath logs, or in underground erosion chambers [36]. In these more hipogaeic species, raids and emigration columns can take place underground but only for short distances and when near the bivouac [53]. Knowledge on *Eciton* army ants is primarily based on research focused on *E. burchellii* and to less extent on *E. hamatum*, as these two species are the most epigaeic diurnal *Eciton* species. Most *Eciton* species are column raiders (e.g. *E. hamatum*, *E. vagans*), with hunting taking place by ants moving initially in narrow columns that later divide into several diverging branches. The size of the raid varies among species, from sparse raid front such as those in *Eciton dulcium,* often narrower than 2 m, to swarm fronts wider than 5 m in in the swarm raider *E. burchellii* [38,53,54].

A large-scale survey conducted at La Selva Biological Station (Costa Rica) examining the diets of sympatric neotropical army ants, including the species *E. burchellii*, *E. dulcium*, *E. hamatum*, *E. lucanoides*, *E. mexicanum* and *E. vagans* revealed high specialisation and small spatio-temporal niche overlap [55]. Using DNA barcoding to identify ant prey to the species level revealed differences in raiding preferences, with *E. dulcium* and *E. mexicanum* preferentially raiding ground-nesting ants and *E. hamatum* and *E. burchellii* arboreal-nesting ants. Furthermore, *E. hamatum* and *E. burchellii* colonies were found to have more diurnal raids whereas most of the other *Eciton* species had primarily nocturnal raids [55].

All *Eciton* species are predominantly predators of other ants (mainly their brood) although they specialise on different ant genera. *E. hamatum* predominantly preys on the brood of *Acromyrmex* leaf-cutting ants, *E. dulcium* on *Pachycondyla* and *Odontomachus* ants, and *E. burchellii* on *Camponotus* ants [14–20]. Although the diet of *E. burchellii* is more varied and includes a diverse range of non-ant litter arthropods, in particular the brood of other social insects [56–61], this non-ant component of the prey might be comparatively low [55]. The large colony size of *Eciton* species, with estimates ranging from 150,000 to 500,000 workers in *E. hamatum* and 500,000 to 2 million workers *in E. burchellii* [38], and the relatively large body size of of some of the workers imply high colony-energy demands [62]. Colonies of *Eciton* army ants have a nomadic-statary cycle, with periods of in which the bivouac (temporary nest) remains in a fixed location where the queen lays thousands of eggs [63]. During this period, the workers hunt prey locally in a regular manner. The statary phase is followed by a nomadic phase coinciding with the eggs hatching into larvae and, during this phase, the colony emigrates daily after the raids over the period of 2–3 weeks [36,64]. In the most studied species, *E. burchellii,* colonies concentrate their raids on invertebrate-rich forest patches [65] and a colony could capture c. 30,000 items of prey in a single day [66]. The nomadic-statary cycle of *Eciton* colonies is interpreted as an adaptation to avoid prey depletion by promoting population recovery of their prey [56]. The pattern of raids, as part of the nomadic lifestyle of *Eciton* army ants, therefore, exerts top-down regulation of leaf litter arthropod communities and creates a mosaic of habitat patches at different ecological succession stages which increases local species diversity [35,65,67].

### 3. Associates of *Eciton* Army Ants

*Eciton* army ants play an important role for the maintenance of biodiversity in neotropical forests not only due to the mosaic habitat that they create as top predators but also due to the hundreds of associate species that depend on these army ants for their survival [36,37,68,69]. The next sections will provide an overview of the main taxonomic groups found with *Eciton* army ant colonies, with a particular focus on arthropods, as this is the most abundant taxonomic group of associates (Figure 1).
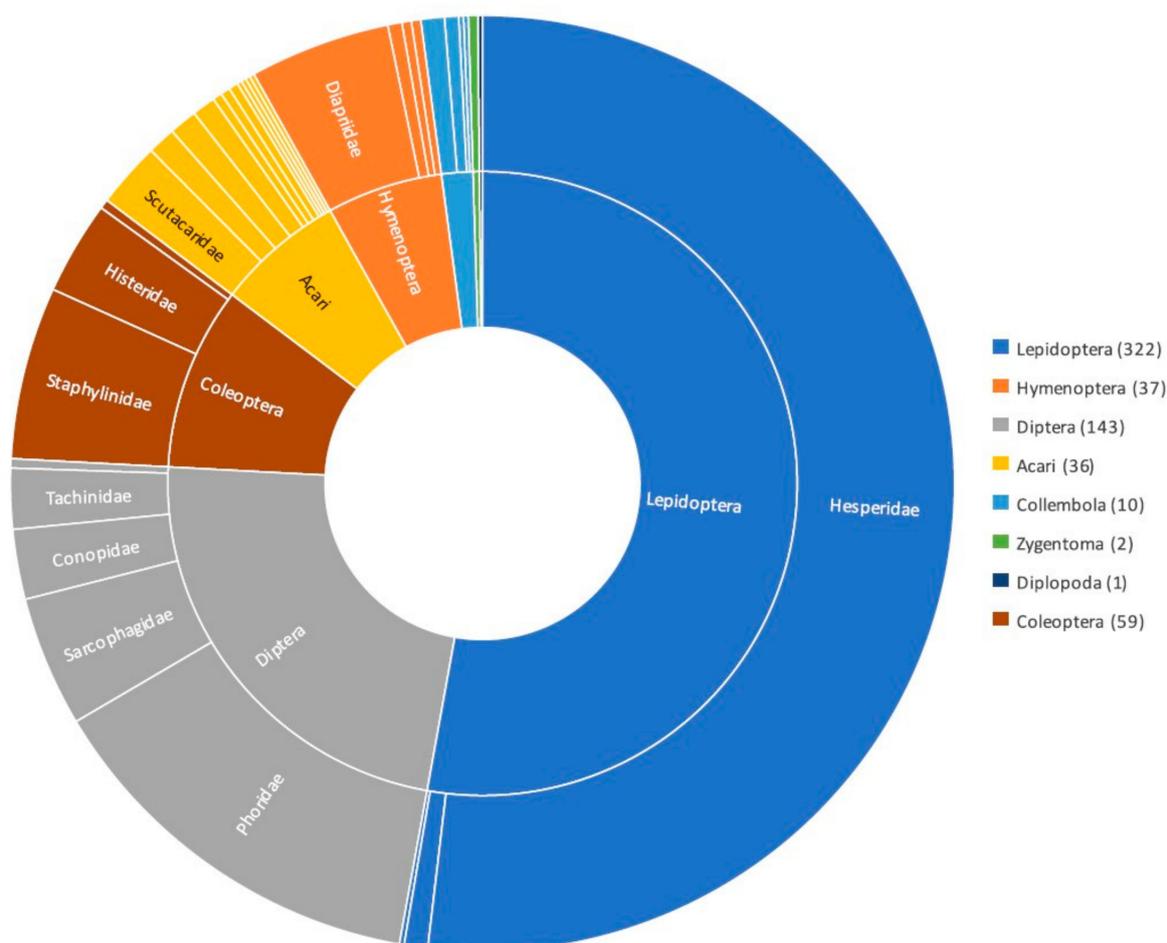


**Figure 1.** Diagram illustrating the different arthropod taxonomic groups found as associates of *Eciton* army ants. Numbers in brackets indicated number of species reported as *Eciton burchellii* associates; data from Rettenmeyer [69]. See Table S2 for further details of families with lower representation within each of the main arthropod taxonomic groups.

#### 3.1. Birds

The majority of studies on associates of *Eciton* army ants have been conducted on the iconic antbirds (Table S1). Army ants provide important foraging resources for antbirds as these primarily feed on arthropods flushed during the ant raids [36,70]. The most commonly reported army ant following birds are within the families Cuculidae, Formicariidae, Furnariidae, Thamnophilidae and Thraupidae, although species from other bird families can also be found at army ant raids [68]; see Table S1. Phylogenetic studies of the Thamnophilidae have revealed that this army ant-following specialisation has evolved three times in this bird family and that this specialization is ancient, with an origin in the late Miocene [71]. Furthermore, the most likely evolution progression of specialisation has been indicated to be from occasional to regular visits, to an obligate association with the army ants (Figure 2).
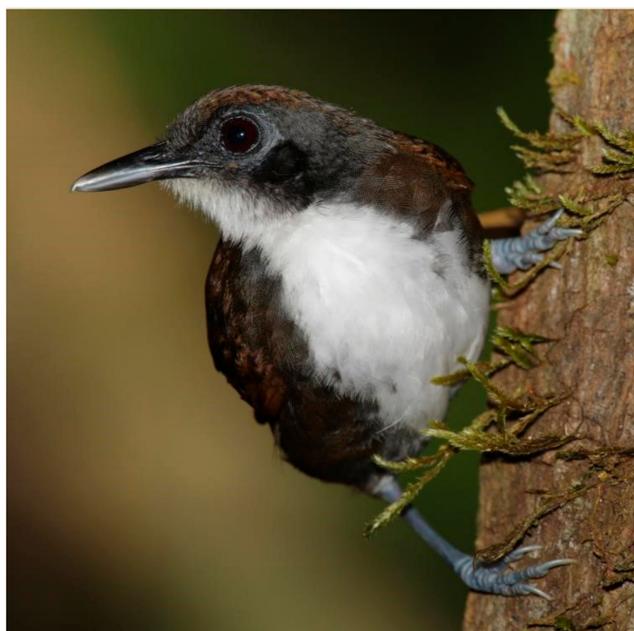
**Figure 2.** The Bicolored Antbird (*Gymnopithys leucaspis*, family Thamnophilidae) is an obligate army ant follower of *Eciton burchellii* colonies. Birds of this species are found at high frequencies at swarms and check bivouac sites. Photo taken at Parque Nacional Darién, Panama (Matt Deres at English Wikipedia, CC BY 3.0).

Antbirds are more commonly found with epigaeic diurnal swarm raid-forming army ants such as *E. burchellii* and *Labidus praedator* [68,69]. Although other *Eciton* species characterised by having column raids, straggling swarm or semi-nocturnal habits might not be important resources for diurnal ant-following birds, reports indicate that antbirds can also be found associated with column-raid army ants when the raids are spread [72]. Antbirds are also occasionally reported with straggling swarms such as those of *E. rapax* [73] and the mainly nocturnal species *E. mexicanum* [72] and *E. vagans* [74]. Screech owls (*Otus* spp.) have also been reported to follow nocturnal raiding army ants in some instances [68].

In addition to the flushed arthropods during army ant raids, antbirds have also been reported to benefit by capturing larger prey such as *Anolis* lizards [75]. The capture of fleeing snakes by Collared forest falcons (*Micrastur semitorquatus*) during *E. burchellii parvispininum* raids has also recently been reported [76]. The association of antbirds with army ants range from occasional visitors to obligate attendants of the raids [68,77–79], see Table S1. Numerous antbirds appear after an army ant raid starts and will then follow the hunting swarm as it advances. Obligate species are likely to track the location of the army ant colonies and some antbirds have been reported to visit statary bivouacs, potentially as a way to monitor colony activity [68,80]. Antbirds are considered parasites of the army ants, as exclusion experiments have indicated a detrimental effect of the antbird foraging on the success rate of prey capturing by ants [81]. Although some field observations [82,83] and gut content analyses [84] have reported the consumption of army ants by antbirds, it is not yet clear if consumption of army ants by antbirds can be intentional in some instances or if this consumption is accidental as most reports indicate [68].

*3.2. Other Vertebrates*

Observations of mammals associated with *Eciton* army ants are limited to marmosets, with five species having been reported to take prey flushed by *Eciton burchellii* in Brasil [85,86]. *Callithrix humelifer* and *C. kuhli* are the species more frequently reported in *E. burchellii* raids, with *C. humelifer* observed to spend several hours picking prey including that being carried by the ants [85]. Other vertebrate species such as the toad *Bufo marinus*,

teid lizards of the genus *Ameiva* and *Kentropyx*, and the iguanid *Anolis frenatus* have also been reported to found associated with *Eciton* army ant raids [68].

### 3.3. Mites

The most numerous associates of *Eciton* colonies, in terms of number of individuals, are mites. It is estimated that myrmecophilous mites found in colonies of army ants within the tribe Ecitonini can be in a ratio > 100:1 to other myrmecophilous arthropods and c. 1:100 to ants in the colony, although in some colonies the ratio can be as high as 1:4 [37]. At least 126 species belonging to 33 different genera of mites have been described in association with army ants in the tribe Ecitonini, 21 of the genera found to be unique to them [87], and 41 taxa found in *E. burchellii* colonies [69]. However, further research is needed to determine if some of these taxa are associated with the army ants or their prey [87].

Some of the mites associated with *Eciton* species can be found either in refuse deposits or middens taking advantage of this food resource (refuse, discarded prey, ant corpses or fungi). However, those thought to be more intimately associated with the army ants are found in the bivouacs and/or emigrating columns [37,69]. Although the nature of the association of the mite taxa with the army ants is yet not well understood, this can potentially be parasitic, mutualistic, phoretic or considered as predators of other taxa visiting the middens [88]. Most of the mite taxa more closely associated with *Eciton* colonies are phoretic, i.e. using the ants as transport agents at least for one stage of their life cycle dispersal, with the phoretic relationship being either facultative or obligatory [38]. Life cycles for mites associated with army ants remain largely unknown but it is likely that they are synchronised with the emigration intervals in *Eciton* host colonies [38]. Phoretic mites have adaptations to be able to ride along with the emigration columns or attach to different parts of the queen, males, different worker castes, and larvae [37,89]. Phoretic mites have also evolved strategies to hitchhike on the ants, such as cuticular ridges on the lateral body flanges developed on adult *Antennequesoma* mites allowing them to attach to *Eciton* workers' antennae or legs [89], or *Planodiscus* mites that their body is sculptured to resemble structures of their *Eciton* hosts to attach to their legs [88,90,91]. Some mites associated with *Eciton* army ants are ectoparasites of brood or adult ants, and feed on the host's hemolymph or integumental secretions, with some species having evolved striking adaptations to attach on different body parts of workers and integrate into the colony [37,87,88]. An example of ectoparasitic mites is *Macrocheles rettenmeyeri* which is found attached on the membrane of hind legs' pulvilli of *Eciton dulcium* workers [92]. The mite's curve hind leg resembles the ant's tarsal claws and, therefore, assumes the function of this body part when the ants hang to one another forming a bivouac [88]. *Rettenmeyerius carli* is another example of ectoparasitic mite, in this case, found attached to the mouthparts of majors [37].

The effects of parasitic mites on *Eciton* colonies are unknown. Inspection of *E. burchellii* workers collected during raid columns from 20 colonies in Barro Colorado (Panama) indicated that mite species diversity was high, with a greater number of mites observed in ants collected in raids during the statary phase [93]. Mite prevalence was of c. 5% (from a total of 3146 ants analysed), with infection found to be higher in larger workers (majors and submajors), and *R. carli* the most commonly found mite on *E. burchellii* workers [93]. However, it is important to highlight that workers in raid columns represent only one-third of the colony [66] and, therefore, prevalence and infection rates might differ in army ants staying in the bivouac [93]. According to mite groups feeding preference classifications [87,94], most of the mites observed in this study were suggested to be relatively harmless for the ants (e.g. fungivore, bacterivore), with only 2 out of the 31 taxa classified with confidence as parasitic (*R. carli*, and an unknown taxon within the family Circocyllibanidae).

### 3.4. Flies

Flies are the second most numerous associates in terms of individuals reported on army ant *Eciton* colonies, with flies within the family Phoridae being the most abundant.

Phorid (or scuttle) flies are found in swarm raids, ant columns, bivouacs and refuse deposits [37,69]. In addition to phorid flies, blowflies (Calliphoridae), thick-headed flies (Conopidae), flesh flies (Sarcophagidae) and tachinid flies (Tachinidae) are also found during *Eciton* raids, in particular in the front or in advance of the swarm fronts. Flies found in *Eciton* raids either hover constantly over the raid or rest on objects with the aim to parasitise insects flashed during the raids. These flies avoid being near the army ant columns or swarms and, similar to other associates, can be either facultative or obligatory [95]. Frequently reported parasitic flies are species within the genera *Androeurops*, *Apocephalus* or *Stylogaster* or *Calodexia* [69,95,96]. Different species of *Androeurops* have been reported attacking crickets and cockroaches flushed during *E. hamatum* and *E. burchellii* raids [37,96]. These flies might be attracted to *Eciton* raids when they detect distress pheromones released from the ants' victims such as found for the phorid *Apocephalus paraponerae* that parasitises the bullet ant *Paraponera clavata* [97]. Phorid flies of the genus *Cremersia* and *Dacnophora* have been shown to parasitise non-*Eciton* neotropical army ants (*Neivamyrmex*, *Nomamyrmex*, and *Labidus*) but there are no records of parasitic flies of *Eciton* army ants [95], although other phorid flies found near the raids might parasitise some *Eciton* associates [95]. In addition to those flies found over or near *Eciton* raids, species within the families Phoridae, Muscidae and Sarcophagidae are commonly found in ants refuse deposits and might be flying between bivouacs to locate these food resources [37].

*3.5. Beetles*

A diversity range of beetles, in particular of the those belonging to the families Staphylinidae and Histeridae, are found associated with *Eciton* colonies either in refuse deposits or in emigration columns [37]. These beetles range from generalists and are found with more than one genus of army ant, e.g. species within the genus *Alloiodites* [37], to host-specific and only found with colonies of a single *Eciton* species, e.g. *Ecitophya*, *Ecitomorpha* [51]. Some beetles are found in refuse deposits feeding either on dead workers or booty refuse, with reports of flying between bivouacs (e.g. *Ecitophora*, *Omalodes*) and/or running in emigration columns (e.g. *Mesynodites*, *Phelister*). Staphylinidae beetles are common in *Eciton* emigration columns, most frequently located at the edges of the column. Beetles found in emigration columns do not attack the ants, except for some predators such as *Tetradonia terminalis* which predates on adult workers of *E. burchellii*, *E. hamatum* and *E. lucanoides* [37,98]. Integrative taxonomic studies, including DNA barcoding approaches, on *Eciton* colonies in La Selva Biological Station (Costa Rica), identified five *Tetradonia* species, including two novel species. Host specificity varied among species, with the generalist *T. laticeps* parasitising six species of *Eciton* to the specialised *T. lizonae* mainly associated with *E. hamatum* colonies [99].

During the procession of associates following *Eciton* emigration columns, the number of beetles is particularly abundant when the brood is carried away from the bivouac. At this phase of the emigration is when the diversity of beetles more intimately associated with *Eciton* colonies can be observed, such as species of the genera *Euxinister*, *Vatesus*, *Cephaloplectus*, *Limulodes*, *Ecitophya* and *Ecitomorpha* [37,100,101]. Among this array of *Eciton*-following beetles, a number of histerid and staphylinid beetles have evolved morphological, chemical and/or behavioural strategies for further integration in the colony. Some species have evolved adaptations to enable them to ride on the different castes. For example, *Pulvinister nevermannii* has been observed riding under the major heads of *E. hamatum* [42,102], *Limulodes* species riding on queens, and some histerids observed riding on males when present in the colony. Some beetle species are found riding on different worker castes, such as *Euxenister wheeleri* found with *E. hamatum* emigration columns, as well as pupae and larvae carried by workers such as *Euxenister caroli* found in emigration columns of *E. burchellii* [37,42,102,103].

Two genera of staphylinids, Ecitomorpha and Ecitophya (Figure 3) are often found in raids, as well as emigration columns of Eciton army ants. These beetles are highly specialised to the nomadic life of Eciton colonies and mimic their media workers [104].

These two genera of staphilinids have evolved similar body modifications to moderately resemble their host, including their colouration [104–106]. The presence of Ecitomorpha and Ecitophya is rare on Eciton colonies, with an estimate presence of less than one beetle per 1000 workers. These beetles are found in raiding columns feeding on dropped prey or booty catches, and, hence, these beetles are considered hunting guests of the army ants [106]. Ecitomorpha and Ecitophya are adapted to the nomadic life of Eciton colonies and are also found in emigration columns, walking in the centre of the column or riding on ant pupae or prey captured by the ants [105,106]. Early taxonomic work on the genera Ecitomorpha and Ecitophya indicated single host-specificity due to their parallel colouration to that of their host [107,108]. However, later taxonomic treatments lumped several species into a single one, due to the difficulties in finding consistent morphological characters, including colouration, to separate species [104,106]. Using an evolutionary and population genetics framework, analyses of mitochondrial DNA sequences of Eciton hosts and their associated Ecitomorpha and Ecitophya, collected in different areas in east and west Panama, revealed that the speciation pattern of these two myrmecophiles was congruent with specialization to a single species (or subspecies) of Eciton host [51]. Molecular clock analyses conducted in this study suggested that Eciton host diversification pre-dated that of their hunting guests, and that Ecitophya have been associated with Eciton for a longer period of evolutionary time than Ecitomorpha [51]. Furthermore, patterns of diversification of the two hunting guests were also consistent across broad geographical areas but not at small geographical scales, with evidence of gene flow between colonies even across large water features [51]. The specialisation of Ecitophya and Ecitomorpha with their Eciton hosts has also been further confirmed by analyses of cuticular hydrocarbons (CHCs) and behavioural analyses of individuals collected at La Selva Biological Station in Costa Rica [109]. In contrast, similar analyses in the staphylinid ant predator Tetradonia indicated that as a generalist, their chemical profile was more dissimilar to their Eciton hosts, compared to that of the specialists Ecitophya and Ecitomorpha [109].



**Figure 3.** The rove beetle *Ecitophya simulans* (family Staphylinidae) moderately mimics of *Eciton burchellii* media workers and is considered a hunting guest. Photo of *Ecitophya simulans* next to an *Eciton burchellii foreli* media worker (Taku Shimada).

Beetles of the genus *Vatesus* (Staphylinidae) are also considered to be intimately associated with *Eciton* army ants. These large and conspicuous limuloid (horseshoe crab-shaped) beetles, and in particular the species *V. clypeatus*, have been observed in *E. burchellii*, *E. hamatum*, *E. vagans*, *E. dulcium* and possibly *E. mexicanum* colonies [42,100,110]. The life cycle of *Vatesus* beetles was suspected to be tightly linked to their *Eciton* hosts, with reproduction and larval development observed to be synchronised to the reproduction and nomadic cycles of their *Eciton* hosts during field studies [37,101,110]. The full life cycle of *Vatesus*, however, was only reconstructed in a relatively recent study using DNA barcoding approaches in which high *Eciton* host-specificity was confirmed and cryptic diversity within the species *V. clypeatus* identified [111].

### 3.6. Other Arthropods

Springtails (Collembola) are abundant in refuse deposits and are represented by a large number of species that might primarily feed on fungi or mould [37,42]. Some species are considered myrmecophilous and also found within the bivouac, in particular those belonging to the subfamilies Cyphoderinae and Paraollinae. The most common myrmecophilous springtails found in *Eciton* colonies belong to the genus *Cyphoda* [37], and two species of *Cyphoderus* have also been reported from *E. burchellii* and *E. hamatum* refuse deposits and suggested as myrmecophiles. However, a large number of springtail taxa found in bivouacs and refuse deposits of *E. burchellii* remain to be identified [37,69].

Millipedes (Diplopoda) of the genera *Calymmodesma* and *Rettenmeyeria* have been reported in *Labidus* and *Nomamyrmex* army ant columns but not in *Eciton* [42,112,113]. Only one species, *Prionodesmus fulgens*, has been reported near bivouac detritus of *E. burchellii* colonies [69].

Silverfish (Zygentoma; previously Thysanura) have been observed in bivouacs, emigration and raid columns of *Eciton* species, in particular species within the genus *Trichatelura* [37]. The species *T. manni* and *T. borgmeiri* are frequently observed running in the centre of the emigration columns when brood is carried from the bivouac, or during nocturnal raid columns where *T. manni* has been also observed to ride on large larvae or booty carried by the ants [37,42]. *Trichatelura manni* has been found associated with different *Eciton* species and observed cleaning and riding on the queens of *E. vagans* and *E. dulcium crassinode* [42]. Observations of *T. manni* in the laboratory conditions confirmed this species as strigilator, feeding on secretions or particles from surfaces of army ant adults, larvae and booty [37,52].

Small wasps of the family Diapriidae are found as associates in *Eciton* colonies [37,114,115], with 17 Diapriidae genera found associated with *Eciton burchellii* colonies [69]. Similar to the mimicry observed in myrmecophilous staphylinids, some of these parasitic wasps have also evolved strategies to integrate into *Eciton* colonies by modifying its form and colour to resemble their *Eciton* host media workers. For example, *Mimopria ecitophila* mimics media workers of *E. hamatum* and it is found in raid and emigration columns of this army ant [42]. These army ant-mimicking wasps are frequently found running in the ant columns and are probably parasites of the army ants or some or their guests [37,42,103,114]. Other Hymenoptera families have also been observed over or near *E. burchellii* colonies or refuse deposits, including other parasitic wasp families such as Scelionidae, Proctotrupidae, and Pompilidae; the latter called spider wasps and suggested to follow the army ant swarms to find spider victims to parasitise [69].

The latest survey of *E. burchellii* associates conducted by Rettemeyer et al. [69] indicated that over 300 butterfly (Lepidoptera) species within the families Hesperiidae, Nymphalidae and Papilionidae were sampled on bird droppings and/or using lures at swarm raids of *E. burchellii*. These butterflies might extract uric acid or partly digested proteins from the bird droppings to be used for egg production [42]. Early field observations of these butterflies, in particular skippers, suggested that *Eciton* colony odours during the raids could resemble male mating pheromones and, therefore, explain the presence of only female skippers [116,117]. However, the recording of male skippers in *E. burchellii* swarm raids casted doubt on the previous hypothesis [118]. A more plausible explanation is that skippers, such as those within the genus *Mechanitis*, are attracted to *E. burchellii* swarm

raid odours as a method of colony detection where they can search for the antbird droppings [119–121]. After observations of the species *Mechanitis polymnia ishtmia*, *M. lysimmia doryssus*, and *Melinea lilis imitata* feeding on droppings from antbirds, in particular from the family Formicariidae, during *E. burchellii* raids, led to coining the term antbutterflies to highlight the close association of these butterflies with this army ant colonies [120]. In addition to the presence of butterflies in *Eciton* raids, microlepidoptera caterpillars have also been reported from refuse deposits [37].

### 3.7. Microbes

The application of DNA metabarcoding approaches has also facilitated recent studies assessing the gut microbiota of army ants. The first initial survey of army ants gut microbiota showed that some ant-specific bacteria clades (e.g. Entomoplasmatales) were shared between three species of neotropical army ants, *E. burchellii*, *Nomamyrmex hartigii*, and *Cheliomyrmex* sp. [122]. This study also found that these bacteria were likely to be associated with the predatory lifestyle of the army ants; although no essential nutritional benefits could be attributed to the presence of these bacteria [122]. A more recent study survey of gut microbiota in army ants including samples from three army ant genera (*Eciton*, *Labidus*, and *Nomamyrmex*) further confirmed a degree of specialisation of certain gut microbial communities in army ants, with the most abundant microbes assigned to Unclassified Firmicutes and Unclassified Entomoplasmatales [123]. Further analyses of these data indicated that gut microbiota variation was found at different levels, between and within species of *E. burchellii* and *L. praedator*, as well as between sympatric colonies *E. burchellii* in Monteverde (Costa Rica), Henri Pittier National Park (Venezuela), and Cocahoatan (Mexico). Variation of gut microbiota composition found in army ants would agree with studies indicating that landscape and local environment can shape gut microbiota in wild insect populations, therefore, explaining geographical variation on microbial profiles [124,125]. One intrinsic challenge faced in DNA metabarcoding of gut contents is our inability to distinguish signatures (in this case DNA sequences) derived from the target species and those of their prey [126]. Therefore, future analyses would benefit from a comparison of gut microbiota of *Eciton* host to those of their potential prey.

### 3.8. Further Research on Eciton Associates

Although a multitude of vertebrate and invertebrate species associated with *Eciton* army ants have been described, substantial research is still required to identify many of the arthropod taxa collected or observed in previous studies [69]. Interdisciplinary integrative taxonomy-focused projects would be crucial to advance the identification and classification of these taxa, the discovery of new species, and elucidation of host specificity [99,127]. Furthermore, reports and studies of associates of *Eciton* army ants have primarily focused on *E. burchellii*. Therefore, further research on associates of other *Eciton* species with different lifestyles, foraging patterns and behaviours (e.g. hypogaeic lifestyle, nocturnal raids) is likely to identify an additional suite of vertebrate and invertebrate associate taxa to those already reported with *E. burchellii*. Beyond research on different *Eciton* species, there is also a need for studies to cover wider geographical areas, as the genus *Eciton* has a wide distribution, from Mexico to Argentina, but studies on associates of these army ants have mainly been restricted to Costa Rica and Panama to date. The creation of a network of researchers ensuring the participation and coordination of research projects by local researchers would facilitate the collection of samples, funding and collaboration needed to increase our understanding of *Eciton* army ants and their associates throughout their distribution range.

## 4. Deforestation and *Eciton* Army Ants

Deforestation and habitat fragmentation are predicted to have negative effects in particular on species at higher trophic levels, higher mobility, greater ecological specialization and representative early diverging lineages [128]. The effects of habitat fragmentation,

therefore, are expected to be more accentuated in top predators such as army ants, with studies on *E. burchellii* indicating negative long-term responses to forest fragmentation [129]. *Eciton* army ants require large forested areas to obtain large amounts of leaf litter prey and maintain their large nomadic colonies, as well as to shelter from higher temperatures encountered in open areas [60,63,130–132]; therefore, making them particularly sensitive to landscape fragmentation and deforestation [34,39]. Simulation studies based on *E. burchellii* colonies on Barro Colorado Island (Panama) estimated that areas of at least 30 ha of continuous forested would be needed to support a single colony of this army ant [39]. This critical area might differ between geographical areas as field-based studies of *E. burchellii* colonies in Mato Grosso (South West Amazonia, Brazil) found that colonies of this species emigrate less frequently than in Barro Colorado Island, possibly due to a larger density of prey in this area [133]. However, other studies on *E. burchellii* colonies have indicated that even when large areas of forest remain after fragmentation, the long-term persistence of colonies is not guaranteed if these patches are not connected by suitable corridors [34,39,56,131,134].

The maintenance and expansion of traditional agrosystems such as shaded coffee and cocoa plantations are considered realistic management actions to address current environmental and socio-economic challenges in neotropical areas [135]. The presence of *Eciton* colonies has been reported in shaded coffee and cocoa plantations, as these habitats provide prey as well as bivouac resources [136–139]. However, the use of shaded coffee and cocoa plantations by *Eciton* colonies might be only temporary and dependent on the availability of non-modified forested areas nearby [136,139,140]. A landscape genetics study of *E. burchellii* colonies in Panama gave further support to the importance of maintaining mature forested areas [141]. This study revealed that deforestation is a major gene flow barrier for *E. burchellii foreli* colonies. In contrast, mature forests were identified as gene flow facilitators. Other forest types, including shaded coffee plantations, were found to act as gene flow facilitators but only when these were located nearby mature forests [141]. The negative effect of deforestation in *E. burchellii* gene flow was also demonstrated in a subsequent landscape genetics study in Costa Rica that revealed that queen relatedness was correlated with land cover, further highlighting the need to maintain connectivity between colonies [142]. Gene flow between colonies was assumed to be primarily by the large winged males when they emerge and fly in large numbers from their colonies in search of mates; *Eciton* queens are wingless and dispersal, therefore, is entirely pedestrian [48]. This male-biased dispersal has also been indicated by genetic studies comparing maternally-inherited mtDNA sequences and biparentally-inherited microsatellite genotyping data from *E. burchellii* colonies [141,143,144]. However, a recent study analysing population structure of *E. b. parvispinum* across years using microsatellite markers indicated that due to the nomadic lifestyle of these army ants, queen dispersal significantly contributes to gene flow and in some instances exceeds that of males [145].

The creation or protection of forested corridors between neighbouring forested fragments has been suggested as possible management actions to facilitate connectivity and longer-term persistence of *E. burchellii* colonies, as thermal ecology studies indicated that high temperatures in open pastures between fragments could prevent the ants to leave their forest patches [131]. These corridors would not only be beneficial to guarantee gene flow between colonies by facilitating queen and colony pedestrian dispersal but also the dispersal of winged males. Although due their nocturnal behaviour, *Eciton* males are less likely to be affected by high temperatures in open areas between forest fragments, flying over open areas increases the risk of predation by nocturnal insectivorous vertebrates [146,147]. Therefore, suitable forest corridors between fragmented areas would facilitate dispersal, and subsequent gene flow, via maternal and paternal lines.

Foraging rates of diurnal epigaeic army ants such *E. burchellii* are lower in open areas compared to forested areas, in particular at lower elevations where these ants might be at their upper limit thermal tolerance threshold [131,132]. Although *E. burchellii* colonies are frequently reported to cross open areas, use remnant forest fragments [131] and heavily overgrown abandoned pastureland [148], even brief exposure to high temperatures can

lead to mortality of their workers [131]. Therefore, movement of colonies between forest fragments might be conditioned by temperature in the environment and vegetation characteristics of the less hospitable matrix between the fragments [131]. The crossing of open areas is feasible during cloudy days or in areas where scattered trees and shrubs can provide shade during the passage [131]. However, mortality among workers during these incursions has been observed after cloud clearing during hottest hours of the day (Pérez-Espona, pers. comm.). For the more hypogaeic and nocturnal species of *Eciton*, such as *E. vagans* and *E. mexicanum*, habitat type does not seem to affect foraging rates, with these increasing with elevation [132].

Ecological assemblages are crucial for the maintenance of ecosystem function and services, and the resilience of these is likely to be dependent on local diversity [149,150]. Local diversity has been shown to be strongly reduced by the destruction or disturbance of the natural environment as a result of land-use changes [151]. In tropical areas, the effect of deforestation and habitat fragmentation has led to a decrease in bird species richness [152]. The dependence of antbirds on army ant colonies make them particularly susceptible to habitat fragmentation. The reduction or disappearance of antbirds from certain forests can be explained by a decrease or absence of important resources such as the presence of army ants [34,129,153–157]. Higher species richness, as well as greater attendance of antbirds following army ants is found in continuous forests [78]. In contrast, antbirds are more prone to local extinction in small forest fragments [155,157]. Considering the numerous associates already reported with *Eciton* army ants, the disappearance of their colonies will not only have a negative effect on antbird local diversity but on the diversity of large number of species across different taxonomic groups.

## 5. *Eciton* Army Ants as Umbrella Species in Neo-Tropical Forests

Data on species richness and abundance is critical to prioritise the establishment of conservation areas [158]. As this information is often absent, and the effort to collect complete datasets would require long-term funded research projects, data on surrogate species – species that provide an indication of biodiversity levels in a particular area – offer an alternative solution to facilitate the establishment of conservation areas [22,159]. The use of surrogate species generally involves gathering data on their diversity and distribution to project the distribution of other less well-known taxa [17,160]. The use of bioindicator groups has often proved successful for identifying patterns of species at large geographical scales [160–162] but their use as predictors for species richness at smaller geographical scales, at which conservation actions take place, has been disputed [17,163,164]. An alternative approach for the delineation of conservation areas at smaller geographical scales is the use of umbrella species. Species categorised as an umbrella require large areas of habitat for their survival and, therefore, by protecting their habitat, many other species will be protected [16,165], including those that share similar ecology [166,167] or those species more directly interacting with them [168]. However, the conservation of these other species is strongly dependent on the appropriate selection of the umbrella species [169,170].

Vertebrates, in particular large predators, have frequently been selected as umbrella species [171]; however, an ongoing debate exists about whether or not the protection of these vertebrates can effectively conserve the habitats and ecosystems where they exist [172]. Invertebrate species have also been used as umbrella species in areas where large iconic vertebrates are absent, with butterflies being the most commonly used in terrestrial ecosystems [168,173]. Furthermore, increasing recognition of the central role of invertebrates, in particular insects, on the functioning of ecosystems has led to their protection as well as to implement their use for the establishment of conservation areas and management plans [21,30,33,168].

It is important to highlight that the value of a particular umbrella species is underpinned by the conservation aims and that, in some instances, multiple species might need to be considered when devising conservation actions to ensure the long-term protection of local biodiversity [168,174]. *Eciton* army ants represent excellent potential umbrella

species for the conservation of neotropical forests. A multitude of species, invertebrate and vertebrate, have already been described to be associated with *Eciton* colonies, with many more species yet to be reported and described [69]. Furthermore, large forested areas are needed for the long-term maintenance of their large colonies not only to guarantee a diverse leaf litter prey community but also to protect *Eciton* colonies from temperatures that hinder their dispersal between forest fragments [34,39,131]. The negative effects of deforestation, habitat fragmentation and land-use change on *Eciton* colonies have been reported by field-based studies [60,175] as well as genetic studies [141,142], indicating the importance of the protection of mature forests for the long-term survival of these army ants, and subsequently, for the many species depending on them. Although there are no available studies assessing any negative impact of the disappearance of *Eciton* colonies in non-associates, the designation of *Eciton* as umbrella species would also ensure the protection of other species in neotropical forests coexisting in the same areas, in particular those that require large extents of forested area for the maintenance of their populations. Therefore, conservation actions aimed to maintain the long-term persistence of army ants, either by identifying areas for protection or creation of habitat corridors to maintain or increase connectivity between *Eciton* colonies in fragmented forests would have positive impact on a wide range of neotropical forest species.

Despite their importance as keystone species in neotropical forests, none of the *Eciton* species, or in fact any other army ants, have yet been considered as umbrella species for the delimitation of conservation areas or for the monitoring of sustainable use in neotropical forests, although their significant influence in ecosystem structure, composition and functioning has been widely recognised [34,176]. The selection of *Eciton* species as umbrella species to identify priority conservation areas or monitor sustainable use could represent an effective and efficient approach for the conservation of neotropical forests and the ecosystem services that they provide. Therefore, this review calls for the consideration of *Eciton* army ant species in future conservation planning, design of nature reserves, and monitoring of sustainable use of forests in neotropical areas, by recognising the key role of *Eciton* species for the maintenance of biodiversity. To successfully achieve the long-term protection of neotropical forests, conservation actions must be led by local researchers and environmental agencies and non-governmental organisations with the participation of local communities that depend on forested areas for their livelihood [177–179].

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