

Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function

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Abstract. 1. Intensive agricultural practices drive biodiversity loss with potentially drastic consequences for ecosystem services. To advance conservation and production goals, agricultural practices should be compatible with biodiversity. Traditional or less intensive systems (i.e. with fewer agrochemicals, less mechanisation, more crop species) such as shaded coffee and cacao agroforests are highlighted for their ability to provide a refuge for biodiversity and may also enhance certain ecosystem functions (i.e. predation).

2. Ants are an important predator group in tropical agroforestry systems. Generally, ant biodiversity declines with coffee and cacao intensification yet the literature lacks a summary of the known mechanisms for ant declines and how this diversity loss may affect the role of ants as predators.

3. Here, how shaded coffee and cacao agroforestry systems protect biodiversity and may preserve related ecosystem functions is discussed in the context of ants as predators. Specifically, the relationships between biodiversity and predation, links between agriculture and conservation, patterns and mechanisms for ant diversity loss with agricultural intensification, importance of ants as control agents of pests and fungal diseases, and whether ant diversity may influence the functional role of ants as predators are addressed. Furthermore, because of the importance of homopteran-tending by ants in the ecological and agricultural literature, as well as to the success of ants as predators, the costs and benefits of promoting ants in agroforests are discussed.

4. Especially where the diversity of ants and other predators is high, as in traditional agroforestry systems, both agroecosystem function and conservation goals will be advanced by biodiversity protection.

Key words. Biological control, cacao, coffee, conservation, function of biodiversity Hymenoptera: Formicidae, sustainability.

Biodiversity and ecosystem function

The relationship between biodiversity and ecosystem function is a topic that has generated intensive research and controversy in recent years (Huston, 1997; Cameron, 2002; Hooper *et al.*, 2005). Most studies focus on the relationship between producers and soil microbes with primary productivity, stability and nutrient cycling, largely neglecting how changes in predator di-

versity may affect ecosystem function (Duffy, 2002). There are several ways, however, in which changes in animal diversity within food webs could change trophic interactions and ecosystem function (Duffy, 2002). Predator and prey diversity change food web structure and predator–prey interactions affecting ecosystem function because consumers have higher per capita impacts on resources (relative to their abundance) than producers. Top-down regulation of communities could be severely limited as predator species are lost due to low functional diversity in the predator trophic level. Increasing predator diversity may increase the likelihood that important predator species are included in the predator community, thereby enhancing predator function (Hooper *et al.*, 2005). Alternatively, presence of each predator species in a diverse group may be important because this assures feeding complementarity – i.e. with more predator

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species, a more diverse range of diets and foraging behaviours are represented resulting in stronger effects on herbivores and plants (e.g. Naeem & Li, 1998; Schmitz & Suttle, 2001; Hooper *et al.*, 2005). Differences in predator species' behaviour and diet may also be important in consideration of the insurance hypothesis of biodiversity function (Yachi & Loreau, 1999). The insurance hypothesis states that although particular species may not appear currently to affect ecosystem function, maintaining diversity may provide long-term stability when environmental conditions change, as they inevitably do. In the context of predation, supporting a functionally diverse predator community including different foraging strategies or diets may enable predator communities to adapt and respond to changing conditions such as pest outbreaks (Hooper *et al.*, 2005). For coffee agroforests, some direct evidence shows diversity can augment ecosystem services (pollination: Klein *et al.*, 2003) yet, separating effects of species richness from abundance is difficult (e.g. Balvanera *et al.*, 2001).

Agroecologists have long known of the importance of diversity for pest control (Swift & Anderson, 1993). Since Elton (1958) warned agricultural intensification would increase pest outbreaks, many have investigated the relationships between plant diversity and predator species richness and abundance in agricultural systems (e.g. Andow, 1991). Predator diversity may increase in more diverse agroecosystems (Altieri *et al.*, 1977; Letourneau, 1987) resulting in better pest regulation (Elton, 1958; Andow, 1991; Provencher & Riechert, 1994). Two hypotheses explaining this phenomenon are (i) the enemies hypothesis that states that generalist and specialist natural enemies are more abundant in polycultures where they thus more efficiently reduce herbivores, and (ii) the resource concentration hypothesis that states that herbivores are more likely to locate and remain on concentrated host plants, such that specialised pests exhibit reduced ability to find and feed on host plants in polycultures (Root, 1973). Andow (1991) reviewed 209 studies reporting that in 109 (52% of the cases), there were lower herbivore population densities on plants in polycultures. Similarly, Dempster and Coaker (1974) reported at least 12 studies showing increased predator abundance in diversified systems reduced various insect pests. These results suggest the resource concentration and enemies hypotheses are complementary in increasing pest control in diverse agroecosystems, and that using natural enemies for pest control has an enormous importance for agroecosystem function.

Agriculture and conservation, the case of shade-grown agroforestry crops

Human activity threatens to generate mass extinction (Tilman *et al.*, 2002) and agriculture exacerbates the extinction problem; approximately 75% of arable lands are now cultivated (McNeely & Scherr, 2003). Agricultural intensification increases threats to biodiversity by creating unsustainable systems highly dependent on external inputs (Shriar, 2000). Biodiverse tropical regions are particularly susceptible to land degradation related to intensification (García-Barrios, 2003). In recent years, conservation biologists have acknowledged the importance of

including agricultural systems into conservation plans for protecting biodiversity. Vegetatively complex agricultural lands incorporating high diversity, density, and height can maintain levels of biodiversity similar to nearby native forests (Moguel & Toledo, 1999), facilitate between-fragment dispersal (Vandermeer & Carvajal, 2001; Steffan-Dewenter, 2002), and may maintain metapopulation dynamics and long-term survival of forest species (Vandermeer & Carvajal, 2001; Perfecto & Vandermeer, 2002).

Two multistrata agroforestry systems highlighted as important to biodiversity are coffee, *Coffea* spp. (Rubiaceae) and cacao, *Theobroma cacao* L. (Sterculiaceae). These systems are particularly noted because of their potential to preserve associated biodiversity (Perfecto *et al.*, 1996; Reitsma *et al.*, 2001), their ability to provide biodiversity refuges in areas with little remaining forest (Perfecto *et al.*, 1996; Moguel & Toledo, 1999), and their role as templates for sustainable agricultural systems (Somarriba *et al.*, 2004). Coffee and cacao intensification, however, results in biodiversity loss. Coffee and cacao were traditionally cultivated under a diverse, dense shade canopy, but recent production is characterised by increased management intensity – reducing shade tree density and diversity, shade tree pruning, and use of agrochemicals (Moguel & Toledo, 1999). Across production systems, traditional, rustic agroforests where crops are grown under a native forest canopy are the most biodiverse (Perfecto *et al.*, 1996; Klein *et al.*, 2002b). Cacao intensification negatively affects the diversity of arthropods (Roth *et al.*, 1994; Klein *et al.*, 2002a; Siebert, 2002), including predators (Klein *et al.*, 2002b). Coffee intensification results in the loss of arthropod biodiversity (Perfecto *et al.*, 1996, 1997; Moguel & Toledo, 1999; Klein *et al.*, 2002a; Perfecto *et al.*, 2003) and affects biological control agents, including ants (Ibarra-Núñez *et al.*, 1995; Lachaud & García Ballinas, 1999). Coffee and cacao agroecosystems are thus models for testing the negative effects of agricultural intensification on biodiversity (Vandermeer & Perfecto, 1997; Moguel & Toledo, 1999; Perfecto & Armbrrecht, 2003) and the negative effects of biodiversity loss on ecosystem services (Perfecto *et al.*, 2004).

Ant diversity and mechanisms of ant diversity loss

Ants are ubiquitous, diverse, and abundant; in tropical ecosystems ants represent up to 80% of animal biomass (Hölldobler & Wilson, 1990). Ants are a major focus for testing hypotheses regarding species richness (e.g. Kaspari *et al.*, 2003), community dynamics and interactions (e.g. Leston, 1973; Gotelli & Ellison, 2002), eco-physiological hypotheses (Kaspari *et al.*, 2000), mutualisms (e.g. Bronstein, 1998), and invasions (e.g. Holway *et al.*, 2002). Ants are also useful as a focal taxon in agroecological research. Certain assemblages of ants including tramp species, forest specialists, and predatory specialists are sensitive to habitat changes such as agroecosystem intensification (Andersen *et al.*, 2002; Bruhl *et al.*, 2003). In addition, ants are sensitive to disturbance and rehabilitation (Andersen *et al.*, 2002), have a straightforward taxonomy (Alonso & Agosti, 2000), and ant diversity shows strong negative responses to

coffee and cacao intensification (Nestel & Dickschen, 1990; Roth *et al.*, 1994; Perfecto & Snelling, 1995; Perfecto *et al.*, 1996, 1997; Roberts *et al.*, 2000; Perfecto & Vandermeer, 2002; Armbrrecht & Perfecto, 2003; Armbrrecht *et al.*, 2005; Philpott *et al.*, 2006). Although other arthropods are more responsive to habitat changes (Perfecto *et al.*, 2003) ants are none the less useful for conservation assessment because of the general ease with which they can be studied, and the other above-mentioned factors.

There are several causal mechanisms proposed in the general ecological literature that may explain losses in ant diversity with coffee and cacao intensification. These can be grouped into physiological and ecological factors. Physiological factors include both microclimatic changes affecting forest-adapted species (e.g. Nestel & Dickschen, 1990; Perfecto & Vandermeer, 1996) and changes in temperature and moisture affecting dehydration-susceptible litter ants (Kaspari & Weiser, 2000). Several ecological factors may influence ant diversity. Species may lack a preferred size, type, or species of nesting site (Leston, 1973; Torres & Snelling, 1997; Roberts *et al.*, 2000; Armbrrecht *et al.*, 2004) or particular species, size, or composition of shade tree necessary for nesting (Greenberg *et al.*, 2000). Ants may also be affected by type, number, and height of microhabitats (Morrison, 1998), or food availability, presumably related to microbial populations and food webs in litter (Kaspari *et al.*, 2000). Ecological interactions that contribute or have the potential to contribute to changes in ant diversity include invasion of exotic ants (Feener, 2000; Holway *et al.*, 2002), competitive exclusion by aggressive ant species frequently abundant in intensive agricultural habitats (Nestel & Dickschen, 1990), predation by army ants (Kaspari, 1996), predation by birds (Philpott *et al.*, 2004), and increased resource access associated with phorid flies parasitising competitive dominants (Feener, 2000; Philpott, 2005).

Of those mechanisms that affect ant diversity in general, nest site limitation has received the most attention specifically with respect to agricultural intensification. Nest site limitation is experienced by many ants and may be exacerbated by agricultural intensification. Shade tree removal accompanying intensification may increase nest-site limitation because litter and twigs from shade trees provide ant nests. In fact, recent studies show twig-nesting ants may be prevented from establishing in low-shade coffee habitats due to limited twig number or diversity (Armbrrecht & Perfecto, 2003; Philpott & Foster, 2005). In Mexico, the proportion of litter twigs with ant nests decreased with distance from forest in a shaded monoculture but not in a neighbouring shaded polyculture suggesting that twig-litter nesting ants are lost with intensification (Armbrrecht & Perfecto, 2003). In these same sites, arboreal ants are somewhat nest-site limited, demonstrated by the fact that they used the majority of available natural nests (dry, hollow coffee twigs) and also that they used a artificial nest sites (bamboo twigs placed on coffee plants); significantly more artificial nests were used in more intensive sites (Philpott & Foster, 2005). Furthermore, more species occupied the artificial nests added to coffee plants (five per plant) than the natural nests (one per plant) indicating that limits in nest site availability may limit diversity. Although tropical ant diversity positively correlates with plant diversity and structure (Roth *et al.*, 1994; Perfecto & Snelling, 1995; Bestelmeyer & Wiens, 1996), until recently it was unclear if litter diversity

affects litter-nesting ant assemblages. In Colombian coffee farms, Armbrrecht *et al.* (2004) found striking evidence that litter twig diversity (from multiple shade tree species) resulted in increased diversity of those ants nesting therein. Importantly, increases in ant diversity were not associated with particular ant–twig species associations, but instead influenced either by emergent properties of twig diversity, such as unknown differences in structural, biochemical, or biological attributes in multi- vs. single-species sets of twig, or by twig diversity *per se*. These results (Armbrrecht *et al.*, 2004; Philpott & Foster, 2005) suggest artificial nests could be used to increase ant diversity and abundance for biological control.

Ants as predators

Examples of ants as biological control agents

Generalist predators, such as ants, are often used as biological control agents of insect pests and fungal pathogens. Tropical ants are predators, scavengers, and generalist foragers (Hölldobler & Wilson, 1990). A recent meta-analysis of studies in agroecosystems found that generalist predators (single- and multiple-species assemblages), controlled herbivore abundance (79% of studies) and reduced plant damage and increased plant yields (65% of studies) (Symondson *et al.*, 2002). Ants, in both natural and agricultural systems (25 of 41 studies), exhibit top-down effects by limiting herbivore communities and by increasing plant growth and reproduction (Schmitz *et al.*, 2000). Ants are biological control agents in agroecosystems and reduce undesirable pests by directly preying upon pests, by chemically deterring them and by causing pests to drop from the host plants that they are attacking (Way & Khoo, 1992). In addition, ants may indirectly reduce herbivore populations, for example, army ants increase movement of arthropods that are then consumed by army-ant following birds (Roberts *et al.*, 2000). Ants also reduce fungal phytopathogens by removing spores (de la Fuente & Marquis, 1999) or by restricting interactions between plants and disease vectors (Leston, 1973; Khoo & Ho, 1992).

The role of ants in coffee and cacao agroforestry systems

Many ant species control cacao pests or fungal diseases (Table 1). For example, the black cocoa ant (*Dolichoderus thoracicus* F. Smith) controls mirids, cacao pod borers, and rat attacks on cacao pods in South-east Asia (Majer, 1976; Khoo & Chung, 1989; See & Khoo, 1996). The weaver ant (*Oecophylla smaragdina* Fabricius) controls mirids (Way & Khoo, 1989) and pod weevils (Stapley, 1973). In Papua New Guinea, *Anoplolepis longipes* Jerdon limits pod weevils (McGregor & Moxon, 1985). In West Africa, *Oecophylla longinoda* Latreille preys on caspids (Leston, 1973; Machart & Leston, 1969). Some species control fungal diseases such as *D. thoracicus* that limits *Phytophthora palmivora* outbreak on cacao pods by reducing disease transmission (Khoo & Ho, 1992). Ants reduce mirid attacks minimising sticky lesions that attract dipteran vectors of *P. palmivora*. Additionally, *O. longinoda* feeds on caspids

Table 1. Documented cases of biological control of insect pests and fungal pathogens by ants in coffee and cacao agroforestry systems.

Ant species	Pest	Common name	Region	Crop	Reference
	Heteroptera: Miridae				
<i>Dolichoderus thoracicus</i> F. Smith	<i>Helopeltis theivora</i> Waterhouse	Mirids	SE Asia	<i>T. cacao</i>	Khoo & Chung (1989)
	<i>Helopeltis theobromae</i> Miller				
<i>Oecophylla longinoda</i> Latreille	<i>Distantiella theobroma</i> Dist.	Caspids	W Africa	<i>T. cacao</i>	Machart & Leston (1969); Leston (1973)
	<i>Salbergella singulares</i> Hagl.				
<i>Oecophylla smaragdina</i> Fabricius	<i>Helopeltis theobromae</i> Miller	Mirids	SE Asia	<i>T. cacao</i>	Way & Khoo (1989)
	Heteroptera: Pentatomidae				
<i>Oecophylla longinoda</i> Latreille	<i>Antestiopsis intricata</i> Ghesquiere and Carayon	Antestia bugs	W Africa	<i>Coffea</i> spp.	Leston (1973)
	Hymenoptera: Formicidae				
<i>Anoplolepis gracilipes</i> Jerdon	<i>Crematogaster</i> spp., <i>Pheidole</i> spp., <i>Camponotus</i> spp.	Ants	Papua New Guinea	<i>T. cacao</i>	McGregor & Moxon (1985)
<i>Oecophylla longinoda</i> Latreille	<i>Crematogaster</i> spp.	Ants	W Africa	<i>T. cacao</i>	Strickland (1951)
	Coleoptera: Curculionidae				
<i>Anoplolepis gracilipes</i> Jerdon	<i>Pantorhytes szentivanyi</i> Marshall	Pod weevil	Papua New Guinea	<i>T. cacao</i>	McGregor & Moxon (1985)
<i>Oecophylla smaragdina</i> Fabricius	<i>Pantorhytes</i> spp.	Cocoa weevil	SE Asia	<i>T. cacao</i>	Stapley (1973)
	Coleoptera: Scolytidae				
<i>Azteca instabilis</i> F. Smith	<i>Hypothenemus hampei</i> Ferrari	Coffee berry borer	Mexico	<i>C. arabica</i>	Perfecto & Vandermeer in press
<i>Dorymyrmex</i> spp.	<i>Hypothenemus hampei</i> Ferrari	Coffee berry borer	Colombia	<i>C. arabica</i>	Velez <i>et al.</i> (2003)
<i>Gnamptogenys sulcata</i> F. Smith	<i>Hypothenemus hampei</i> Ferrari	Coffee berry borer	Colombia	<i>C. arabica</i>	Velez <i>et al.</i> (2003)
<i>Pheidole</i> spp.	<i>Hypothenemus hampei</i> Ferrari	Coffee berry borer	Colombia	<i>C. arabica</i>	Velez <i>et al.</i> (2003)
<i>Solenopsis</i> spp.	<i>Hypothenemus hampei</i> Ferrari	Coffee berry borer	Colombia	<i>C. arabica</i>	Armbrrecht (2003)
<i>Tetramorium</i> sp.	<i>Hypothenemus hampei</i> Ferrari	Coffee berry borer	Colombia	<i>C. arabica</i>	Armbrrecht (2003)
	Lepidoptera: Gracillariidae				
<i>Dolichoderus thoracicus</i> F. Smith	<i>Conopomorpha cramerella</i> Snellen	Cacao pod borer	SE Asia	<i>T. cacao</i>	Khoo & Chung (1989)
	Rodentia: Muridae				
<i>Dolichoderus thoracicus</i> F. Smith	<i>Rattus argentiventer</i> Robinson and Kloss	Rice-field rat	SE Asia	<i>T. cacao</i>	See & Khoo (1996)
	Fungal phytopathogens				
<i>Dolichoderus thoracicus</i> F. Smith	<i>Phytophthora palmivora</i> Butler	Pod rot and canker	SE Asia	<i>T. cacao</i>	Khoo & Ho (1992)
<i>Oecophylla longinoda</i> Latreille	<i>Calonectria rigidiuscula</i> Berk. and Br.	Pink disease	W Africa	<i>T. cacao</i>	Leston (1973)

thereby controlling *Calonectria rigidiuscula*, which attacks where caspids have fed (Leston, 1973).

Relatively few studies investigate the role of ants in coffee agroecosystems, but some ants are known to be beneficial (Table 1). In West Africa, *O. longinoda* limits coffee antestia bugs (Leston, 1973). *Solenopsis geminata* Fabricius, an important biological control agent in some areas (Risch & Carroll, 1982; Perfecto & Sediles, 1992) often dominates sun coffee plantations but does not prey on coffee berry borers (*Hypothenemus hampei* Ferrari) either in Costa Rica (Varon, 2002) or in Colombia (Velez *et al.*, 2003, Gallego & Armbrrecht, in press). *Gnamptogenys sulcata* F. Smith, a shade-loving ant, however, does prey effectively on this pest (Velez *et al.*, 2003) as do several other ant species (Armbrrecht, 2003; Perfecto & Vandermeer, in press). Finally, ants may protect coffee via indirect interactions with other predators. Coffee systems except sun coffee support army ants and up to 126 species of ant-following birds (Roberts *et al.*, 2000). Many birds limit herbivores (Greenberg *et al.*, 2000; Philpott *et al.*, 2004), thus army ant presence may indirectly benefit coffee further showing direct connections between crop

diversity and associated beneficial fauna. Two studies show ants potentially protect coffee from pest outbreaks (Vandermeer *et al.*, 2002; S. Philpott, unpublished data). In both studies, larvae that were introduced on to coffee plants with ants (*Azteca instabilis* F. Smith, *Camponotus senex textor* F. Smith, or *Crematogaster* spp.) were removed significantly faster than on plants without ants. Individual ant species thus act as important predators in coffee and cacao agroecosystems, but few studies summarise how the loss of ant diversity with intensification of these multistrata systems may affect their role as predators.

Effects of ant diversity on predation

Individual ant species can control herbivores or fungal diseases, but determining the importance of ant diversity to biological control is not yet proven. There are several mechanisms by which ant diversity may be important. Ants differ substantially in resource use, with some species garnering more energy from nectar or honeydew, from arthropods, or from different types of

arthropods (Davidson *et al.*, 2003; Philpott *et al.*, 2004). Foraging strategies and recruitment behaviours of ant species also differ (Hölldobler & Wilson, 1990; S. Philpott, *unpublished data*). In studies investigating the effects of three ant genera on introduced larvae (S. Philpott, *unpublished data*), each ant showed different responses to larvae of different species and sizes providing additional evidence that ant diversity may provide a range of responses to unpredictable outbreaks. Intra-specific differences in foraging or behaviour may augment overall responses to herbivore communities (Schmitz & Suttle, 2001; Duffy, 2002) or may increase functionality under the insurance hypothesis (Yachi & Loreau, 1999). At least one empirical example demonstrated that higher bird diversity resulted in increased effectiveness against a pest outbreak in coffee agroecosystems (Perfecto *et al.*, 2004). In this case, bird abundance was also greater in sites with higher bird richness, making it difficult to separate the relative contributions of abundance and richness and thereby potentially enhancing those observed effects attributed to increased richness (Huston, 1997). None the less, the practical significance of increased pest control by increases in bird biodiversity (including richness and abundance) is the same (Perfecto *et al.*, 2004). Benefits of species diversity in functionality may be due to a particular species in a suite, or some inherent property of diversity itself (Armbrecht *et al.*, 2004; Hooper *et al.*, 2005) with the end result of an increase in ecosystem service provided.

Ants: cryptic herbivores or top predators?

Explaining the function of ants in ecosystems is important for agroecology because ants can be perceived by farmers either as dangerous pests or as beneficial predators of pests. Even though they may control pests, several ant species (*Anoplolepis longipes*, *Azteca* spp., *Oecophylla* spp., and *Wasmannia auropunctata* Roger) are avoided or controlled because they bite human workers in plantations (Haines & Haines, 1978; Way & Khoo, 1989; Delabie, 1990; Ulloa-Chalon & Cherix, 1990). The most harmful perception (with respect to agriculture) that most farmers and ecologists have relates directly to ant–homopteran associations. Two non-mutually exclusive hypotheses explain how ant biomass (and activity) are maintained: (i) ants are cryptic herbivores tending trophobiont homopterans and feeding from extrafloral nectaries (EFNs) (Hunt, 2003), or (ii) ants are predators and cause high turnover of canopy herbivores (Floren *et al.*, 2002). If ants function more as homopteran-tenders, ants will harm crop plants. Yet because ants also function as predators, the benefits of homopteran-tending may outweigh costs. Below is a focus on the experimental evidence for both costs and benefits relative to pest control.

Ants form mutualistic associations with homopterans, whereby ants harvest honeydew (a sugary homopteran exudate) and protect homopterans from predators and parasitoids (Way, 1963), move homopterans to better feeding sites (Way, 1963; Buckley, 1987), or improve conditions for homopteran offspring (Nixon, 1951). Ants are problematic to farmers because: (i) large homopteran populations reduce plant fecundity or increase plant mortality (Way, 1963; Banks & McCauley, 1967);

(ii) homopterans vector many viral diseases (Way & Khoo, 1992); and (iii) ants interfere with biological control efforts. For example, in coffee farms, ants defend scale insects (Hemiptera: Coccidae) from natural enemies. Ants protect coccids from natural enemies (Gonzales-Mendoza, 1951), defend red scales (*Saissetia coffeae* Walker) from coccinellid beetles (*Azya luteipes* Mulsant) (Coleoptera: Coccinellidae) (Anonymous, 1990), and protect green scales (*Coccus viridis* Green) from coccinellid and nitidulid predators (Hanks & Sadof, 1990). But does the majority of ant energy come from homopterans?

Some evidence shows ants are cryptic herbivores taking the majority of their energy from homopterans. Davidson *et al.* (2003) tested how much of the ant diet consists of honeydew and nectar by analysing nitrogen isotope ratios of ants collected haphazardly from tropical rainforest leaf litter and foliage in Peru and Brunei; the lighter stable isotope (^{14}N) is lost more readily through metabolic waste and thus the isotopic ratio ($^{15}\text{N}/^{14}\text{N}$) will increase as more prey from higher trophic levels are consumed. They concluded that arboreal ants obtain little nitrogen through predation/scavenging and behave as exudate-foragers (i.e. cryptic herbivores). This conclusion, which might energetically explain why canopy ants defend three-dimensional territories (Hunt, 2003) implies that homopteran densities in canopies are much higher and forest floor prey densities lower than previous experimental measurements indicate. Blüthgen *et al.* (2000) searched for ants feeding at homopterans or EFNs in 66 tree canopies in the Venezuelan Amazon. The proportion of trees on which they found ants feeding at EFNs was very low (0.08% of tree genera) in the canopy (Blüthgen *et al.*, 2000) relative to 34% of understory tree species found in light gaps in Barro Colorado Island, Panama (Schupp & Feener, 1991). None the less, although a much higher proportion of tree species (62% and 83% of genera) had ant-tended homopterans, fewer ant species tended homopterans (16) than were associated with EFNs (52) (Blüthgen *et al.*, 2000). Of ant-tending homopterans, 74% were ants that build carton nests (*Azteca*, *Dolichoderus* and *Crematogaster* spp.), suggesting a few arboreal ant species dominate canopy homopterans. Furthermore, nearly all homopterans (up to 700 membracids and 3000 coccids per tree) were ant-tended (Blüthgen *et al.*, 2000). Ant–homopteran associations thus constitute a major force regulating trophic structure and ant distributions (Blüthgen *et al.*, 2000; Dejean *et al.*, 2000; Davidson *et al.*, 2003).

Although ant–homopteran associations are undoubtedly important, determining the costs of homopteran-tending raises several issues. First, ants may use the majority of captured protein from the canopy to feed larvae, and the samples of adult ants used by Davidson *et al.* (2003) would thus be biased towards a sugar-rich diet. Second, the social gut of foraging ants used in Davidson *et al.* (2003) could be full of honeydew explaining similar isotopes ratios of ants and trophobionts. Third, regardless of whether canopy ants eat canopy arthropods, some are certainly harassed by ants and fall to the forest floor where other components of the predatory ant community could incorporate this protein. Fourth, ant diets may change seasonally; ants may be more predatory if actively producing larvae. Trophic classification of tropical ant genera shows that 72 genera are predators, 31 generalist foragers, 12 fungi growers, six

homopteran-tenders, three seed harvesters, three nectar harvesters, two pollen eaters, two scavengers, and one genus is parasitic (Brown, 2000). Thus more tropical ant genera are predators than all other trophic guilds combined. In Davidson *et al.* (2003) 92% of all Formicinae tested belonged to *Camponotus* and 95% of Dolichoderinae tested were *Azteca* and *Dolichoderus* – all are generalised foragers, although *Azteca* visits EFNs and tends homopterans (Brown, 2000). These two subfamilies represented 43% of all species evaluated in Peruvian samples, suggesting samples were somewhat biased toward generalists. One interpretation is that Davidson *et al.* (2003) demonstrated that nitrogen isotope ranges of exudate-dependent ants resemble those of arthropod herbivores, not that all canopy ants behave as cryptic herbivores. Only 36 of 108 species analysed matched isotopic ranges of sap-feeding trophobionts in Peru (44 matched predator arthropods) and 15 species of 84 in Brunei (26 matching predators). Furthermore, Floren *et al.* (2002) found that 85% of ant species found in 54 non-myrmecophyte trees killed introduced caterpillars and two-thirds of ants sampled from 69 fogged trees were predators. Nevertheless, a few canopy ant species usually constitute the bulk of biomass (e.g. Armbrrecht *et al.*, 2001) and an accurate assessment of ant diets should be done before drawing final conclusions about their role in tropical food webs. One important caveat of the argument presented here, of course, is that the taxonomic diversity of particular trophic guilds does not necessarily reflect the total biomass of each group, and determining the relative biomass of each feeding group would be very interesting. These observations are not intended to undermine the importance of ant–homopteran relationships. For instance, 114 ant–homopteran associations involving 30 ant species and 12 homopteran species were recently reported in Colombian coffee plantations (Franco *et al.*, 2003). Yet most homopterans reported are innocuous for farmers and none are considered insurmountable pests.

Several studies have examined the relationship between ant–homopteran mutualisms and predation by ants. In several cases, the predation by ant species attracted to host plants by homopterans benefits plants enough to outweigh costs of homopteran colonies. Way and Khoo (1992) include ant–homopteran relations among the ecological features of predator ants beneficial for pest management because such relations attract predator ants to specific foraging sites. Several empirical studies show increased plant fitness when resident homopterans attract ants that then deter other herbivores (Dixon, 1971; Room, 1972; Nickerson *et al.*, 1977; Messina, 1981). Increases in herbivore removal associated with homopteran-tending ants result in increased plant growth (Room, 1972) and plant reproductive output (Messina, 1981). Furthermore, Dixon (1971) hypothesised homopteran presence on plants maintains ants that can deter other more damaging herbivores. Ants are part of management programmes in Vietnamese agroforests (Van Mele & Van Lenteren, 2002), even though the species involved (*D. thoracicus* and *O. smaragdina*) tend trophobionts (Van Mele, pers. comm.). Sweeter honeydew (induced by ant foraging) might also attract more parasitoids (Van Mele, pers. comm.), which may parasitise crop pests, thereby reducing plant damage. Two studies in coffee agroecosystems are similarly suggestive of the indirect benefits of homopteran tending. In a study in tradi-

tional coffee plantations, Vandermeer *et al.* (2002) found *Azteca* ant activity, significantly correlated with green scale (*Coccus viridis* Green) concentration on plants, caused a significant reduction of introduced lepidopteran larvae suggesting these ants might provide benefits as predators that could outweigh the damage done by tended scale insects. Furthermore, Perfecto and Vandermeer, in press) studied interactions between *Azteca* ants, green scales, and the economically important coffee pest, the coffee berry borer (*Hypothenemus hampei* Ferrari) (Coleoptera: Scolytidae). On plants with *Azteca*, they found those with fewer scale insects had significantly higher numbers of berries attacked by the berry borer, suggesting that the ant–scale mutualism provides a positive indirect benefit to coffee plants by limiting the primary coffee pest (Perfecto & Vandermeer, in press).

Conclusions

A decline in ecosystem services in tropical agroforests and other managed systems is an extremely important issue relating to biodiversity loss. Conserving both the associated fauna within tropical agroforests and surrounding forest fragments with high-quality agricultural matrices is critical. Ecological concepts such as those considering that ants are either cryptic herbivores or top predators (or both) must be interpreted carefully for the careful and beneficial management of diverse agroecosystems. Yet it is essential that agroecosystem manipulations include a rigorous understanding of each specific system to avoid disillusionment from farmers and abandonment of environmentally friendly agricultural practices. Ants are important predators, and may aid pest prevention and management if well understood and studied.

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