

3 Living Together in Novel Habitats: A Review of Land-Use Change Impacts on Mutualistic Ant-Plant Symbioses in Tropical Forests

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Introduction

Mutualisms form between species when individuals provide reciprocal benefits, increasing the fitness of both partners. Ants and plants often form such mutualistic relationships, with ants providing protection from herbivory, protection from competition from other plants, seed dispersal, CO₂ and/or food, and receiving in return housing space and/or food from plants (Rico-Gray & Oliveira, 2007). Some associations are symbiotic (i.e. partners live together) while in others ants receive food benefits, but nest elsewhere. In this review we focus on ant-plant symbioses (i.e. in which entire colonies of ants inhabit plants), since these tend to be more intimate associations, sometimes have high interaction specificity, and have clearly defined partners. Although symbioses usually involve ants inhabiting plant-evolved living spaces, this is not always the case, with ants sometimes inhabiting other structures (such as the leaf litter layer in litter-collecting species) but nonetheless providing benefits to the plant in terms of protection from herbivory (Gibernau et al., 2007; Fayle et al., 2012) or nutrients (Watkins et al., 2008). For the purposes of this chapter, we exclude ants using plants as attachment points for external nests such as those inhabiting carton structures. Symbiotic ant-plant mutualisms are particularly abundant in tropical forests (Bruna et al., 2005; Feldhaar et al., 2010), where they can play important roles in structuring ecosystems (Frederickson et al., 2005; Tanaka et al., 2009).

* We are grateful to William A. Foster, who supervised ECT, TMF and KMY for their PhDs, during which much of the work on bird's nest ferns reviewed here was conducted, and to Nico Blüthgen, Paulo S. Oliveira and an anonymous reviewer for suggestions that improved the manuscript. TMF was funded by a Czech Science Foundation Standard Grant (16-09427S), CW by a Malaysian Ministry of Higher Education Fundamental Research Grant (FRG0373-STWN-1/2014), KMY by the Universiti Malaysia Sabah new lecturer grant scheme (SLB0071-STWN-2013), and ECT by the Isaac Newton Trust, Cambridge, PT Sinar Mas Agro Resources and Technology Tbk and the Natural Environment Research Council (NE/K016377/1). All authors are also grateful for support by the South East Asian Rainforest Research Partnership.

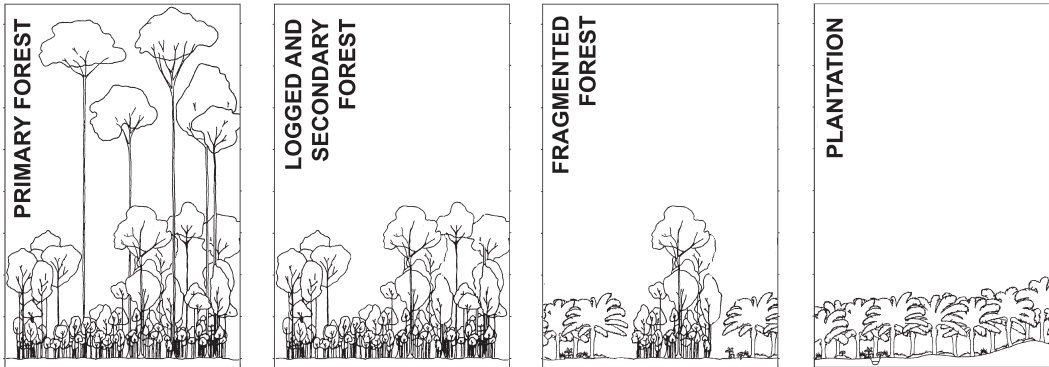


Figure 3.1. Typical habitat conversion gradient for tropical forests. Note that there are two categories of continuous non-primary forest, combined here for brevity: logged forest, which is primary forest with timber selectively extracted, and secondary regrowth forest, which has regenerated following complete clearance (our definitions). The dominant agricultural habitat type varies globally, but is here depicted as oil palm plantation. Figure modified from Foster et al. (2011). Original drawings by Jake Snaddon.

Human-driven land-use causes changes to ecosystems worldwide, driven in the tropics mainly by logging of forests, clearance for expansion of agricultural land, and consequent fragmentation of remaining forest (Tilman et al., 2001; Edwards et al., 2014; Figure 3.1). Although the negative impacts of these processes on the number and identity of species are moderately well-known, changes in species interaction networks are much less studied despite being of key importance (Kaiser-Bunbury & Blüthgen, 2015). This is because network structure can determine community stability in the face of further disturbance (Dunne & Williams, 2009) and therefore affect associated ecosystem processes (Tylianakis et al., 2010).

Symbiotic ant-plant networks are abundant in tropical forests and hence are likely to be affected by habitat disturbance (Mayer et al., 2014). However, remarkably little work has been dedicated to understanding how these networks respond to human-driven land use change (Table 3.1). More specific symbioses can serve as model systems for understanding the altered selective environments in converted habitats (Laughlin & Messier, 2015), while less specific symbioses can be used as microcosms for understanding larger-scale community responses (Fayle et al., 2015b). In the following section we review studies investigating shifts in communities of ant-inhabited plants as a result of selective logging, clearance followed by secondary regrowth, forest fragmentation, and conversion of forest to agriculture. We also speculate on how other anthropogenic impacts, such as altered climate, nutrient enrichment, and invasion by non-native species, might interact with these land-use changes.

The Impacts of Logging, Forest Fragmentation, and Conversion to Agriculture on Ant-Plant Symbioses

Logging of Tropical Forest and Secondary Regrowth Following Clearance

Although it is unlikely that ant-plants are ever directly targeted for removal during commercial selective logging activities, since they tend to be epiphytes or small plants with hollow stems, felling and extraction of trees often damages the surrounding vegetation and may, therefore, indirectly affect them (Picard et al., 2012). Secondary regrowth forests, as distinct from those that have been selectively logged, also have substantially altered vegetation structure (Chazdon, 2014). Furthermore, disturbed forests differ from primary forests in having hotter, drier microclimates, and a more open vegetation structure (Hardwick et al., 2015), potentially affecting both ants and their plant hosts.

As a result of these changes, the density of ant-plants changes over time following disturbance. For example, ant-inhabited *Macaranga*, a common group of ant-plants on the island of Borneo, show an increase in density shortly after complete clearance, peaking after five years, followed by a decrease (Tanaka et al., 2007), presumably due to competition between the *Macaranga* saplings and shading by later succession species. This pattern is also seen for ant-plants in the new world tropics, where *Cecropia* in secondary regrowth increases in abundance following burning of pasture (anecdotal report; Fonseca, 1999). It is worth noting that both of these ant-plant genera, which are among the most widespread and species-rich in their respective areas, are mainly early succession pioneers that specialize on disturbed areas (Fonseca, 1999; Slik et al., 2003). In some cases, logging and regrowth has also been recorded to alter ant inhabitation. For example, *Macaranga bancana* showed lower ant inhabitation rates in secondary forest, possibly due to increased queen mortality or differences in the species of ant inhabitants (Murase et al., 2003). In Papua New Guinea, interaction networks have also been found to differ between primary forest and secondary regrowth, following clearance for food gardens, with substantial reductions in ant-inhabitation of plants (Klimeš et al., 2012; Chapter 2; note that partner benefits have not been demonstrated in this system). However, to our knowledge only one study has directly assessed the impacts of selective logging on symbiotic ant-plant mutualisms, finding no change in the relationship between epiphytic bird's nest ferns and their ant inhabitants (Fayle et al., 2015a, see also the following section). If there are differences in the occupancy and identity of ant inhabitants as a result of logging, then this could have negative impacts on plant survival (Murase et al., 2010), leading to further changes in the community.

Forest Fragmentation

Human-driven expansion of non-forest habitats often results in increasingly fragmented forest patches. This process increases the proportion of forest experiencing changes in community composition and alteration of the abiotic environment near

boundaries between habitats. These ‘edge effects’ can penetrate far from habitat boundaries (Ewers & Didham, 2008), and hence affect a large proportion of the world’s forests (Haddad et al., 2015). Fragmentation also isolates populations in the remaining habitat islands, disrupting migration and potentially leading to long-term ‘extinction debt’ (Laurance et al., 2011). For example, fluctuations in the size of smaller isolated populations can eventually lead to local extinction of these species from individual fragments. Fragmentation is of particular concern for species involved in obligate mutualisms, because persistence in fragments requires the presence of both partner species. Hence these populations are expected to be vulnerable to localised stochastic extinction of one partner, with recolonisation of fragments requiring simultaneous colonisation by both partners (Fortuna & Bascompte, 2006). Furthermore, co-existence between symbiont ant species in undisturbed habitats may rely on dispersal-fecundity trade-offs in combination with variation in host plant density, with species that are highly fecund but poor dispersers dominating in high plant density areas, and vice versa (Yu et al., 2001). Isolation of forest patches substantially changes the distribution of ant-plants, and hence is likely to result in extinction of ant species with poorer dispersal abilities.

Ant-plants have been documented extensively in the Biological Dynamics of Forest Fragments Project (BDFFP) in the Brazilian Amazon, in which forest fragments have been experimentally isolated since 1979 (Laurance et al., 2011). After 25 years of fragmentation, species richness of both ants and plants, overall densities of plants (Bruna et al., 2005) and network structure (Passmore et al., 2012) remain similar to those in continuous forest, suggesting that these systems are remarkably robust to the effects of change. This stability might relate to the proximity of nearby forest, which at 100 m is within the dispersal range of at least some ant species (Bruna et al., 2011), and hence would allow maintenance of sink populations in fragments. There has also been forest regrowth in the cleared areas surrounding the fragments (Laurance et al., 2011), potentially facilitating migration of ants and plants. The nature of the matrix habitat between the fragments (pasture in the case of the BDFFP), is likely to affect the persistence of ant-plant populations in these areas. This is demonstrated by the stronger impacts on ant-plant populations of fragmentation from inundation due to damming of a river, where fragments are isolated by water, rather than pasture (Emer et al., 2013). In this study from the Amazon basin the authors found a reduction in species richness of both ants and plants, and a reduction in compartmentalisation of networks in islands. Smaller and more isolated fragments were less compartmentalised (i.e. networks were not divided into groups of species, with many links within groups, but few links between groups). This is despite fragmentation having occurred only ~10 years prior to the study, and the majority of islands being ~100 m from the nearest mainland or large island. Interestingly, sites on the edges of continuous areas of forest were intermediate between isolated islands and non-edge forest in terms of ant-plant communities, suggesting that symbiotic ant-plant networks are susceptible to edge effects. In the longer term it is possible that the effects of fragmentation on ant-plant interactions and stochastic extinction of populations may

Table 3.1 Summary of Known Impacts of Human-Driven Habitat Change on Ant-Plant Symbiotic Networks

Habitat change type	Plant taxa	Ant taxa	Location	Habitat(s)	Habitat change	Main conclusions	Reference(s)
Logging or forest clearance with regrowth	<i>Teijsmanniodendron</i> , <i>Horsefieldia</i> , <i>Ficus</i> , <i>Macaranga</i>	<i>Anonychomyrma</i> , <i>Camponotus</i>	Papua New Guinea	Lowland rain forest	Clearance for food gardens and secondary regrowth	For trees larger than 5 cm DBH, ant inhabitation of live trees is much less common in secondary forest than primary forest.	Klimes (chapter 2); Klimes et al. (2012)
	<i>Asplenium nidus</i> , <i>A. phyllitidis</i>	Many	Malaysian Borneo	Lowland rain forest	Selective logging	Ferns and ants persist, with ants commonly inhabiting ferns, and ferns being protected by ant residents. No differences between primary and logged forest.	Fayle et al. (2015)
	<i>Macaranga bancana</i>	<i>Crematogaster</i>	Malaysian Borneo	Lowland rain forest	Conversion to secondary forest,* cultivated land or grassland	More saplings inhabited by non-partner <i>Crematogaster</i> species in secondary forest than primary forest.	Murase et al. (2003)
	<i>Cecropia</i>	<i>Azteca</i>	Brazilian Amazon	Pasture	Regrowth following burning and abandonment of pasture	Anecdotal account of forest regeneration, with <i>Cecropia</i> ant-plants dominant. Initially many, small ant-plants, with later thinning out as plants grow. <i>Cecropia</i> dominate the overstory for > 10 years, and are then replaced by later succession trees.	Fonseca (1999)
Forest fragmentation	<i>Hirtella</i> , many others	<i>Allomerus</i> , <i>Azteca</i> , others	Brazilian Amazon	Lowland rain forest	Experimental forest fragmentation, by pasture	No overall changes in density of plants, and little change in network structure, but some plant species become less abundant.	Bruna et al. (2005); Passmore et al. (2012)

Clearance for agriculture	<i>Hirtella, Maietia,</i> many others	<i>Allomerus,</i> <i>Pheidole,</i> others	Brazilian Amazon	Lowland rain forest	Forest fragmentation from dam creation	Reduction in the number of plant and ant species and colonisation rates. Increase in opportunistic species colonising.	Emer et al. (2013)
	<i>Myrmecodia,</i> <i>Hydnophytum</i>	<i>Iridomyrmex,</i> others	Papua New Guinea**	Lowland rain forest, lower montane forest	Conversion to plantations and other artificial habitats	More ant-plant species in disturbed than undisturbed habitats in lowlands, opposite in highlands. More species of ant in <i>Myrmecodia</i> in undisturbed lowlands, opposite for <i>Hydnophytum</i> . More species of ant in <i>Myrmecodia</i> in disturbed highlands, very few species of ant in <i>Hydnophytum</i> in highlands (note: as very small number of species, no formal analyses conducted).	Huxley (1978)
	<i>Asplenium nidus,</i> <i>A. phyllitidis</i>	Many	Malaysian Borneo	Lowland rain forest	Conversion to oil palm	Ferns and ants persist across all habitats, but ant species different in oil palm. Ants still protect ferns. Lower ant abundances in ferns of a given size in oil palm.	Fayle et al. (2010); Fayle et al. (2015)
	<i>Hohenbergia,</i> <i>Aechmea</i>	Many	Bahia, Brazil	Atlantic Forest	Conversion to cocoa agroforest	Introduction of agroforestry decreases interaction specificity, but epiphytes still allow maintenance of similar levels of ant diversity compared to pristine habitat.	DaRocha et al. (2016)

* Authors do not state if these areas were cleared completely and then allowed to regrow, or if they result from selective logging and subsequent regeneration.

** Papua New Guinea and nearby areas.

have wider ranging effects on the whole ecosystem, a speculation supported by the low densities of some ant-plant species in fragments (Bruna et al., 2005). However, the high degree of specificity in many ant-plant systems might protect the system from catastrophic collapse, since the impacts of extinctions of individual species are unlikely to spread through the entire ant-plant network (Passmore et al., 2012).

Conversion to Agricultural Land

Conversion of forest to agricultural land has a greater negative impact on animal and plant communities than degradation of forest (Gibson et al., 2011). In these habitats, ant-plants can usually survive only in unmanaged areas such as habitat margins, or as epiphytes on plantation trees. An example of the latter is the persistence of epiphytic bird's nest ferns (*Asplenium nidus*) in oil palm plantations in Malaysian Borneo, where ferns continue to host ants, which continue to protect the fern from herbivores (Fayle et al., 2015a, see also further pages). Persistence of ant-epiphyte symbioses in food gardens and open areas has also been reported in Papua New Guinea, with response to disturbance depending on elevation (Huxley, 1978). Partial conversion to agriculture has a less extreme impact on ant-plant symbioses. For example, cocoa agroforest, in which native shade trees are maintained, has similar overall levels of bromeliad-dwelling ant diversity to unconverted habitat, although with lower interaction specificity (DaRocha et al., 2016).

Synergy of Land-Use Impacts with Other Human-Driven Global Changes

Other anthropogenic global changes are likely to interact with the effects of differing land-use (Sala et al., 2000), with potential consequences for ant-plant symbioses. Habitat conversion has the potential to exacerbate the impacts of climate change, since increases in temperature due to logging and conversion to agriculture are often much greater than those predicted under even the most pessimistic climate change scenarios (Foster et al., 2011). Impacts of climate change on ant-plant communities can currently be extrapolated only from space-for-time surveys of ant-plants along existing climatic gradients (Mayer et al., 2014). For example, at lower altitudes in Papua New Guinea there is higher species richness of both plants and ants, and evidence for a higher level of plant protection by ants (Plowman et al., 2017). The relative importance of direct climate effects and plant protection by ants has also been investigated through transplant experiments across altitudinal gradients. In a study ranging from lowland Amazonian rain forest to montane Andean vegetation, ant-plants (*Piper immutatum*) were transported outside of their existing range both with and without their symbiotic ants (*Pheidole* sp.). Plant survival was most affected by direct climatic effects, rather than inhabitation or protection by the ant partner (Rodríguez-Castañeda et al., 2011). Extrapolating from these few studies to predict climate change impacts is challenging, because ant-plant responses

will depend on multiple interacting factors, such as migration rates of the mutualistic partners, and whether ranges are defined by biotic or abiotic factors.

Nutrient enrichment may also affect ant-plant mutualisms, especially those that involve provision of nutrition from ants to plants. If plants have greater available nutrients, then ant-provided nutrients will be less valuable (Mayer et al., 2014). Such effects are likely to be greater in agricultural habitats where fertilisers are used, and in adjacent forest areas affected by fertiliser drift (Weathers et al., 2001). However, in some cases nutrient concentrations can also decrease with increasing habitat disturbance, due to depletion of the organic layer or leaching (Fernandes & Sanford, 1995; Owusu-Sekyere et al., 2006), potentially increasing the value of ant nutrient provisioning. It is therefore likely that responses are system-specific and more studies are needed for generalisations to be drawn.

Ants number among some of the most successful of invasive species, causing severe impacts on the functioning of many natural ecosystems (Lowe et al., 2000). Human-altered habitats are often highly susceptible to invasion by non-natives (King & Tschinkel, 2008) and hence ant-plant mutualisms in these habitats are likely to be affected by these newcomers (Chapters 12–15). The outcome of such interactions depends on whether (1) invasive ant species out-compete native plant ants, or (2) native ants are somehow buffered against the invaders, for example by having access to resources provided by plants that invasive ants are unable to utilise (Ness & Bronstein, 2004). As an example of the former scenario, the little fire ant, *Wasmannia auropunctata*, has been documented invading the domatia of the tree *Barteria fistulosa* in secondary forests in Gabon, and consequently reducing occupation by the native ant *Tetraoponera aethiops*. This has resulted in an increase in liana coverage on the trees, as lianas are usually removed by the native ant partner (Mikissa et al., 2013). Ant-plants themselves can sometimes also become invasive species, opening up the possibility of new relationships being formed with native ants from the invaded habitat. For example, Neotropical *Cecropia* plants, which are ant-inhabited in their native ranges, thrive elsewhere, with populations in Hawaii (*C. obtusifolia*) and Peninsula Malaysia (*C. peltata*). In this case, however, plants generally do not contain ants, despite abundant non-specialist ant partners inhabiting *Cecropia* in its native range. This may be because access holes into domatia have not been made by the plant's regular ant partner and also because an absence of specialist herbivores has ensured that lack of protection is not a significant cost to the plants (Putz & Holbrook, 1988; Wetterer, 1997). In general, it seems likely that the degree of interaction specificity will influence the manner in which non-native species of ants and plants interact. With accelerating habitat change, movement of products around the world, and the impacts of climate change taking effect, we are likely to see the formation of further new combinations of ant and plant partners in the future. Understanding the costs and benefits for partners in these novel symbioses is likely to be a fruitful future research direction, informing both core ecological knowledge as well as habitat management strategies for biodiversity and ecosystem services.



Figure 3.2. Bird's nest fern (*Asplenium nidus*) in the high canopy of lowland Dipterocarp rain forest in Malaysian Borneo. The largest ferns reach 200 kg wet weight (Ellwood & Foster, 2004) and can support diverse arthropod communities, including multiple colonies of co-existing ants. Inset photograph shows a colony of ant belonging to the genus *Diacamma*, one of many species that excavate nesting cavities in the root mass of these ferns. Main photograph credit Chien C. Lee; inset Tom Fayle. (A black-and-white version of this figure will appear in some formats. For the color version, please refer to the plate section.)

The Interaction between Epiphytic Bird's Nest Ferns and Ants as a Model System

The interaction between epiphytic bird's nest ferns (*Asplenium* spp.) and their ant symbionts serves as a useful model system for exploring impacts of habitat change on mutualistic interactions. Here we review the current state of research regarding these ferns and their ant symbionts.

Bird's nest ferns are common throughout the old world tropics (Holttum, 1976). They are litter intercepting epiphytes (Figure 3.2; Fayle et al., 2008), probably

deriving the majority of their nutrient requirements from the decomposition of falling leaves that are collected in a broad rosette of fronds (Turner et al., 2007). In lowland Dipterocarp rain forest in Malaysian Borneo, there are two common species of bird's nest fern: *A. phyllitidis* and *A. nidus* (Fayle et al., 2009). *A. phyllitidis* is restricted to more shaded areas, where the continuous canopy layer provides more living space for this species. *A. nidus* is more abundant in areas that are open at ground level and where there are higher densities of emergent trees, since both of these areas provide the open habitat that this species requires. This leads to a vertical stratification, with *A. phyllitidis* being found only below 30 m, but *A. nidus* being found at all heights in the canopy, up to 60 m in the tallest emergent trees. Both species collect leaf litter, and the resulting mass of decomposing organic material, held together by the fern's root mass, is damp and cool, with temperature being buffered compared to that in the surrounding canopy (Turner & Foster, 2006; Freiberg & Turton, 2007). This refuge from the hot, dry rain forest canopy is an attractive habitat for a range of animals (mainly arthropods), the most abundant of which are the Coleoptera, Isoptera, Collembola, Acari, Diptera and Formicidae (Floater, 1995; Rodgers & Kitching, 1998; Walter et al., 1998; Ellwood et al., 2002, 2009; Karasawa & Hijii, 2006a, 2006b; 2006c; Turner & Foster, 2009; Rodgers & Kitching, 2011). As a result of this, the ferns can substantially increase the overall arthropod biomass that an area of canopy supports (Ellwood & Foster, 2004). Furthermore, bird's nest ferns occasionally provide nesting sites for birds (Thorstrom & Roland, 2000; Roland et al., 2005) and stingless bees (N. Blüthgen, personal communication, 2016), roosts for bats (Hodgkison et al., 2003) and habitats for frogs (Scheffers et al., 2013; Scheffers et al., 2014) and earthworms (Richardson et al., 2006). The ferns also co-occur with other epiphytic plant species, which can use the fern's mossy core as a substrate (T. M. Fayle personal observation, 2006), although it is not clear if these aggregations are 'ant gardens', in which ants have planted seeds to strengthen nest structure. Marasmioid fungi, which play a role in the decomposition of leaf litter (Snaddon et al., 2012), are also found in 36 per cent of the ferns in the litter held in the fern rosette (30 of the 83 ferns from Fayle et al. (2012), and the ferns also support communities of fungi and bacteria (Donald et al., 2017).

The most abundant animal group found in bird's nest ferns are the ants, comprising on average 86 per cent of individuals, and 91 per cent of biomass of all arthropods in primary forest ferns in Borneo (Turner & Foster, 2009), although in larger ferns termites are sometimes even more abundant than ants (Ellwood et al., 2002). Multiple ant colonies can co-exist within the litter-root mass (note that ferns do not grow domatia for ants), with larger ferns supporting more ant colonies; up to 12 resident ant species in larger ferns (Fayle et al., 2012). There is considerable ant species turnover between ferns, with at least 71 species across 27 genera using the ferns as nesting sites in primary forest. The identity of these ant species depends weakly on the height of the fern within the rain forest canopy, and on the size of fern, but once these factors are taken into account, there is no difference in ant composition or species richness between the two fern species, *A. nidus* and *A. phyllitidis*. Furthermore, some ant species found in leaf litter on the forest floor also inhabit the ferns (Fayle et al., 2015a). This indicates that the symbiotic

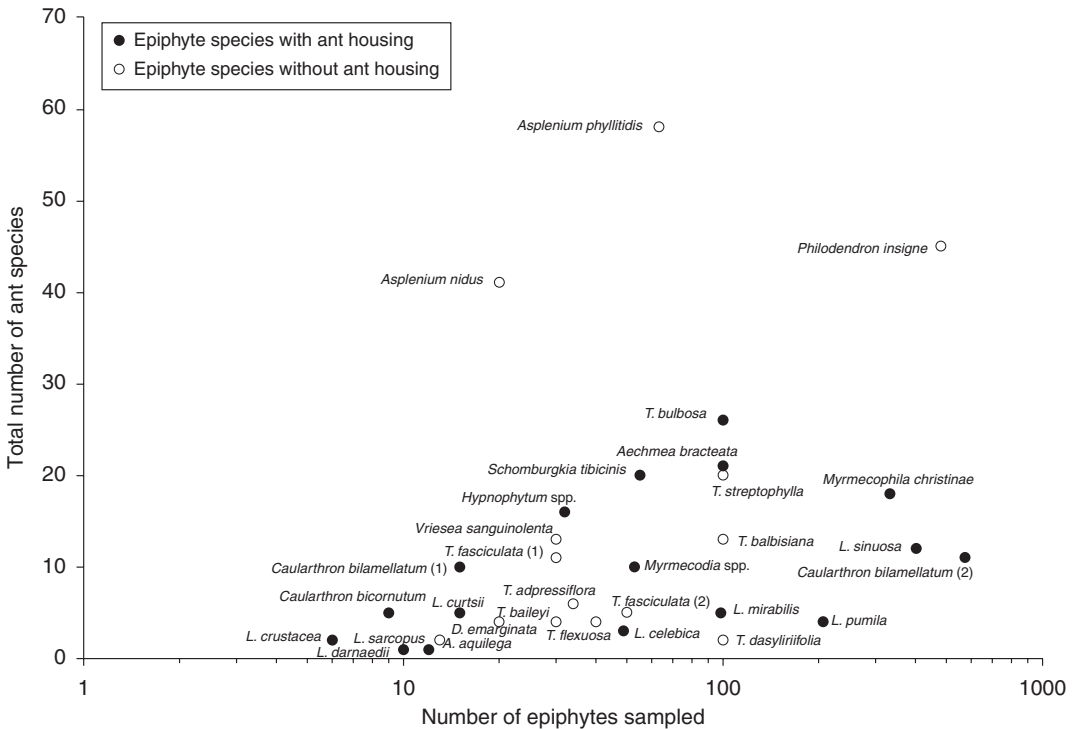


Figure 3.3. Number of different symbiotic ant species found inhabiting epiphytes plotted in relation to sampling intensity and presence of ant housing. Some genus names are abbreviated for clarity: *Tillandsia*, *Leucanopteris*, *Dimerandra*, *Aechmea*. Two species are represented twice, denoted numerically in brackets. Data from publications for which both sampling intensity and number of ant species were reported for ant-epiphyte systems in habitats unmodified by humans (Huxley, 1978; Fisher & Zimmerman, 1988; Gay & Hensen, 1992; Dejean et al., 1995; Blüthgen et al., 2000; Stuntz et al., 2002; Dejean et al., 2003; Gibernau et al., 2007; Dutra & Wetterer, 2008; Fayle et al., 2012; Talaga et al., 2015). Figure reproduced and updated from supplementary online material of Fayle et al. (2012), with permission from John Wiley and Sons.

relationship is non-specific. This is a similar pattern to that observed for some ant-inhabited bromeliads (Blüthgen et al., 2000), where interactions have low specificity compared to a range of other systems (Blüthgen et al., 2007). This low specificity results in the ferns supporting more ant species than epiphytes that grow structures adapted for housing ants, although many other species lacking housing also have low ant diversity (Figure 3.3). The diverse ants inhabiting bird's nest ferns compete with one another for nesting space within the ferns (Ellwood et al., 2016), with species that have more similar body sizes competing most strongly (Fayle et al., 2015b). This competition controls fern-dwelling ant species abundance distributions.

Both ferns and ants receive by-product benefits from their symbiosis. The ants protect the fern from herbivory (Fayle et al., 2012), although this seems to be a result of normal foraging behaviour, with resident ants failing to aggressively

defend ferns from disturbance (T. M. Fayle, personal observation), as would be expected in a protection mutualism. However, the presence of one ant species in the genus *Monomorium* has a negative impact on herbivory rates (Fayle et al., 2015a). An unidentified species in the same genus has also been observed to actively protect *Asplenium nidus* in India, while tending to coccids that mimic the fern's sori (clusters of spore-containing bodies) (Patra et al., 2008). Despite this protective behaviour, this species of *Monomorium* is not particularly common (15/83 ferns; 18 per cent) and the protective effect from herbivores remains even when this species is removed from analyses, indicating that multiple ant species provide this by-product service to the ferns. The lack of a tight mutualistic relationship is probably because there is little incentive for resident ants to promote fern growth, since larger ferns support more species of ants, rather than larger colonies of particular species (Fayle et al., 2012). This failure on the part of the fern to direct benefits towards more beneficial ant species probably arises because ferns are constrained to maintain a leaf litter layer and a soil root mass, which can be inhabited by a wide range of ant species as well as other taxa. Such a situation can be contrasted to those in which plants create pre-formed domatia, in which the increased intimacy of the interaction creates greater opportunities for partner selection and punishment (Edwards et al., 2006). Furthermore, the ferns have not been observed to provide food to their ant inhabitants, and *Asplenium* are not recorded as ever having foliar nectaries (www.extrafloralnectaries.org/). Hence, although ferns and ants receive by-product benefits from the symbiosis, neither partner has adaptively increased investment in the relationship, resulting in a two-way by-product mutualism. This interaction can be seen as an old world parallel to ant-bromeliad interactions in the Neotropics, with both groups being highly abundant, comprising some leaf-litter-collecting species, and showing low specificity of ant inhabitants (Blüthgen et al., 2000).

Throughout the tropics, but particularly in SE Asia, expansion of oil palm plantation following logging is a major driver of forest clearance (Wilcove et al., 2013). Surprisingly, bird's nest fern populations are resilient to habitat change, with abundances decreasing in logged forest, but increasing in oil palm plantation (90, 53 and 117 ferns per hectare in primary forest, logged forest and oil palm plantation respectively (Turner, 2005; see also Padmawathe et al., 2004). However, only the high canopy species *A. nidus* survives in oil palm plantations, perhaps due to its pre-adaptation to hot and dry environments (Fayle et al., 2011). Despite substantial reductions in total arthropod abundance (67.2 per cent decrease) and biomass (87.5 per cent decrease) between ferns in primary forest and those in oil palm plantation (Turner & Foster, 2009), the numbers of species of ants per fern do not change (Fayle et al., 2010). This is in contrast to leaf litter and canopy communities more broadly, which both show substantial reductions in ant species richness. However, in oil palm plantations, a completely different set of ant species inhabit the ferns. The oil palm fern ants show stronger species segregation (consistent with the existence of interspecific competition) than those in primary forest. This pattern is not driven by the presence of non-native ant species (Fayle et al., 2013), with analyses in which non-native species are removed showing even stronger patterns of

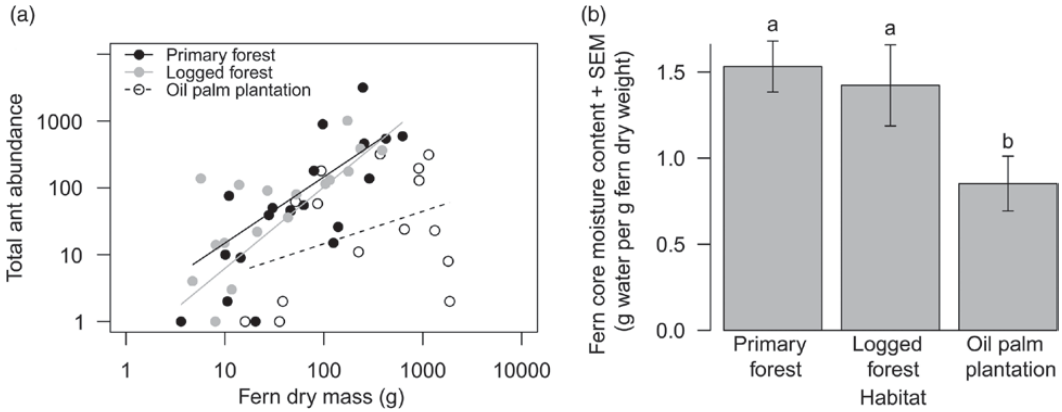


Figure 3.4. (a) The volume of suitable nesting space for ants in ferns differs between habitats, with ferns in oil palm plantation supporting lower total abundances of ants per unit dry weight than ferns from forest habitats. (b) One explanation for this is that ferns in oil palm plantations have significantly lower moisture content than those in either primary or logged forest. Standard error bars are shown. Reproduced with permission from Fayle et al. (2015a).

species segregation. This effect is even more pronounced for ants in the ferns than in the rest of the canopy. The degree of specificity of the interaction remains low in logged forest and in oil palm plantation, with oil palm showing even greater overlap between fern-dwelling and litter ants than the other two habitats (Fayle et al., 2015a). Furthermore, the positive relationship between the fern size and the number of ant species observed in primary forest ferns (Fayle et al., 2012) persists in both logged forest and in oil palm plantation (Fayle et al., 2015a), and there is also no relationship in these habitats between the size of colonies of individual ant species and fern size. This indicates that there is little opportunity for partner fidelity feedbacks in human-modified habitats. Hence, neither ferns nor their resident ants invest in partner fitness, since for the ants, this would not result in benefits being fed back to that colony, and for plants there remains no opportunity to direct benefits to better partners. Interestingly, the relationship between total ant abundance (not that for any particular colony) and fern size differs between oil palm plantation and logged or primary forest, with a given increase in fern size resulting in a much smaller increase in total ant abundance in oil palm plantation (Figure 3.4a). This is probably because the hotter, drier microclimate in oil palm plantations (Turner & Foster, 2006) results in a lower moisture content in oil palm ferns (Figure 3.4b), leading to a reduction in the habitable volume of the fern. Non-native species in oil palm plantation, which are common in the ferns, play a significant role in driving the relationships between fern size and ant species richness/abundance. This indicates that the persistence of this two-way by-product mutualism in oil palm plantations depends to some extent on non-native species. The result also raises the question as to whether more generalist interactions are more robust to habitat change.

Future Research Directions

As the review has demonstrated, this is an area with a paucity of studies. However, ant-plant symbioses offer useful model systems for understanding network responses to disturbance and shifts in costs and benefits for symbiotic partners. Fruitful work could be conducted in a range of different directions.

Differential Responses of Specialised and Generalised Species to Habitat Change

Generalist species are predicted to be better able to persist in human-modified habitats than specialist species, because they are less likely to suffer total loss of all partner species and because they are likely to form new connections more easily. Ant-plant symbiotic systems present an opportunity to test this prediction. For example, a similar pattern has already been found in terms of spatial turnover of ant-EFN bearing plant interactions within one habitat type, with a central core of generalists (those species interacting with many other species) remaining unchanged over larger spatial scales (Dáttilo et al., 2013). With regard to forest fragmentation impacts on networks involving more specialised species, impacts are observed to be greater where ants and plants cannot cross matrix habitats (Bruna et al., 2005; Passmore et al., 2012; Emer et al., 2013). Furthermore, for a less specialised interaction, the symbiosis persists, even in plantation habitats (Fayle et al., 2015a), partly because non-native species are able to take the place of native ant partners. It is also possible that in disturbed habitats there might be some ‘rewiring’ of the network, with persisting species forming novel connections with each other (in addition to interacting with newly arrived species). Hence we predict that the responses of specialist and generalist mutualists will depend on (1) landscape connectivity with source populations of ants and plants, (2) whether non-native species can take the place of native partners for less specialised interactions and (3) the degree to which the network ‘rewires’ itself following disturbance.

Impacts of Abiotic Changes on Costs and Benefits of Interactions

Shifts in the abiotic environment that occur during habitat conversion, such as changes in temperature and nutrient availability, are expected to alter the outcomes of mutualistic interactions, specifically in relation to the value of investing in partners. For example, if converted habitats are more nutrient-poor, then the value of hosting plant-feeding ants will increase; if a hotter habitat means that a smaller volume of the plant is habitable, this may break the relationship between ant colony size and plant size, reducing the value for ants of investing in plant growth (for an example specifically relating to bird’s nest ferns see Figure 3.4 and the section ‘Synergy of Land-Use Impacts with Other Human-Driven Global Changes’). In converted habitats, if species persist, they do so in an adaptive landscape very different from the one in which they evolved (Laughlin & Messier, 2015). Hence robustness to habitat change will depend on species’ abilities to respond plastically over short time periods. It would be worthwhile measuring costs and benefits for partners directly in

relation to changes in various abiotic variables along habitat disturbance gradients. Such measurements could allow better prediction of persistence of species involved in mutualisms. Over longer time periods, tracking evolutionary changes in mutualistic behaviours in converted habitats would also be of interest.

Impacts of Changes in the Biotic Environment

Symbiotic ant and plant species experience novel biotic environments as a result of human-induced changes, both in terms of their partner species and other species that impact on the interaction. For example, non-native *Cecropia peltata* (that are ant-inhabited in their native range) in Peninsula Malaysia experience less herbivory than plants in their native range, despite lacking ant inhabitants (Putz & Holbrook, 1988), perhaps due to a release from specialist herbivores. This represents a radical change in the benefits of ant-inhabitation. A similar pattern is observed when large mammalian herbivores are excluded from *Acacia* ant-plants in Kenya, with the benefits of ant-inhabitation being reduced (Palmer et al., 2008). Hence, even in supposedly pristine habitats, previous mammalian herbivore extinctions might leave mutualistic partners behaving sub-optimally. It would be worthwhile exploring how costs and benefits vary across habitat disturbance gradients both with partner identity and in relation to the presence of other interacting taxa, such as herbivores.

Conclusion

The world's tropical forests are changing rapidly as a result of human disturbance. This not only causes species extinctions at local and global scales, and shifts in species composition, but also drives a re-organisation of interactions between those species that persist. Understanding the nature of these novel interaction networks is vital if we are to maintain ecosystem functioning in human-modified landscapes. Here we have described how mutualistic symbioses between ants and plants are altered when humans exploit tropical forests, although a lack of studies makes generalisation of results challenging. Ant symbioses with bird's nest ferns serve as a useful model system for exploring the impacts of habitat change on non-specific mutualistic interactions. Future research might profitably compare responses to habitat change for mutualistic species with a range of degrees of interaction specificity, and assess the way that costs and benefits of the interaction change in relation to shifts in both abiotic and biotic environments.

References

- Blüthgen, N., Menzel, F., Hovestadt, T., Fiala, B. and Blüthgen, N. (2007). Specialization, constraints, and conflicting interests in mutualistic networks. *Current Biology*, 17, 341–346.
- Blüthgen, N., Verhaagh, M., Goitia, W. and Blüthgen, N. (2000). Ant nests in tank bromeliads – an example of non-specific interaction. *Insect. Soc.*, 47, 313–316.

- Bruna, E. M., Izzo, T. J., Inouye, B. D., Uriarte, M. and Vasconcelos, H. L. (2011). Asymmetric dispersal and colonization success of Amazonian plant-ants queens. *PLoS ONE*, 6, e22937.
- Bruna, E. M., Vasconcelos, H. L. and Heredia, S. (2005). The effect of habitat fragmentation on communities of mutualists: Amazonian ants and their host plants. *Biological Conservation*, 124, 209–216.
- Chazdon, R. L. (2014). *Second Growth: The Promise of Tropical Forest Regeneration in an Age of Deforestation*. Chicago: University of Chicago Press.
- DaRocha, W. D., Neves, F. S., Dáttilo, W. and Delabie, J. H. C. (2016). Epiphytic bromeliads as key components for maintenance of ant diversity and ant–bromeliad interactions in agroforestry system canopies. *Forest Ecology and Management*, 372, 128–136.
- Dáttilo, W., Guimarães, P. R. and Izzo, T. J. (2013). Spatial structure of ant-plant mutualistic networks. *Oikos*, 122, 1643–1648.
- Dejean, A., Durou, S., Olmsted, I., Snelling, R. R. and Orivel, J. (2003). Nest site selection by ants in a flooded Mexican mangrove, with special reference to the epiphytic orchid *Myrmecophila christinae*. *Journal of Tropical Ecology*, 19, 325–331.
- Dejean, A., Olmsted, I. and Snelling, R. R. (1995). Tree-epiphyte-ant relationships in the low inundated forest of Sian Ka'an biosphere reserve, Quintana Roo, Mexico. *Biotropica*, 27, 57–70.
- Donald, J., Maxfield, P., Murray, D. and Ellwood, M. D. F. (2017) How tropical epiphytes at the Eden Project contribute to rainforest canopy science. *Sibbaldia: The Journal of Botanic Garden Horticulture*, 14, 55–68.
- Dunne, J. A. and Williams, R. J. (2009). Cascading extinctions and community collapse in model food webs. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 364, 1711–1723.
- Dutra, D. and Wetterer, J. K. (2008). Ants in myrmecophytic orchids of Trinidad (Hymenoptera: Formicidae). *Sociobiology*, 51, 249–254.
- Edwards, D. P., Hassall, M., Sutherland, W. J. and Yu, D. W. (2006). Selection for protection in an ant-plant mutualism: host sanctions, host modularity, and the principal-agent game. *Proceedings of the Royal Society B: Biological Sciences*, 273, 595–602.
- Edwards, D. P., Tobias, J. A., Sheil, D., Meijaard, E. and Laurance, W. F. (2014). Maintaining ecosystem function and services in logged tropical forests. *Trends in Ecology & Evolution*, 29, 511–520.
- Ellwood, M. D. F., Blüthgen, N., Fayle, T. M., Foster, W. A. and Menzel, F. (2016). Analysis of pairwise interactions reveals unexpected patterns in tropical ant communities *Acta Oecologica*, 75, 24–34.
- Ellwood, M. D. F. and Foster, W. A. (2004). Doubling the estimate of invertebrate biomass in a rainforest canopy? *Nature*, 429, 549–551.
- Ellwood, M. D. F., Jones, D. T. and Foster, W. A. (2002). Canopy ferns in lowland dipterocarp forest support a prolific abundance of ants, termites and other invertebrates. *Biotropica*, 34, 575–583.
- Ellwood, M. D. F., Manica, A. and Foster, W. A. (2009). Stochastic and deterministic processes jointly structure tropical arthropod communities. *Ecology Letters*, 12, 277–284.
- Emer, C., Venticinque, E. and Fonseca, C. R. (2013). Effects of dam-induced landscape fragmentation on Amazonian ant-plant mutualistic networks. *Conservation Biology*, 27, 763–773.
- Ewers, R. M. and Didham, R. K. (2008). Pervasive impact of large-scale edge effects on a beetle community. *Proceedings of the National Academy of Sciences*, 105, 5426–5429.

- Fayle, T. M., Chung, A. Y., Dumbrell, A. J., Eggleton, P. and Foster, W. A. (2009). The effect of rain forest canopy architecture on the distribution of epiphytic ferns (*Asplenium* spp.) in Sabah, Malaysia. *Biotropica*, 41, 676–681.
- Fayle, T. M., Dumbrell, A. J., Turner, E. C. and Foster, W. A. (2011). Distributional patterns of epiphytic ferns are explained by the presence of cryptic species. *Biotropica*, 43, 6–7.
- Fayle, T. M., Edwards, D. P., Foster, W. A., Yusah, K. M. and Turner, E. C. (2015a). An ant-plant by-product mutualism is robust to selective logging of rain forest and conversion to oil palm plantation. *Oecologia*, 178, 441–450.
- Fayle, T. M., Edwards, D. P., Turner, E. C. et al. (2012). Public goods, public services, and by-product mutualism in an ant-fern symbiosis. *Oikos*, 121, 1279–1286.
- Fayle, T. M., Eggleton, P., Manica, A., Yusah, K. M. and Foster, W. A. (2015b). Experimentally testing and assessing the predictive power of species assembly rules for tropical canopy ants. *Ecology Letters*, 18, 254–262.
- Fayle, T. M., Ellwood, M. D. F., Turner, E. C. et al. (2008). Bird's nest ferns: islands of biodiversity in the rainforest canopy. *Antenna*, 32(1), 34–37.
- Fayle, T. M., Turner, E. C. and Foster, W. A. (2013). Ant mosaics occur in SE Asian oil palm plantation but not rain forest and are influenced by the presence of nest-sites and non-native species. *Ecography*, 36, 1051–1057.
- Fayle, T. M., Turner, E. C., Snaddon, J. L. et al. (2010). Oil palm expansion into rain forest greatly reduces ant biodiversity in canopy, epiphytes and leaf-litter. *Basic and Applied Ecology*, 11, 337–345.
- Feldhaar, H., Gadau, J. and Fiala, B. (2010). Speciation in obligately plant-associated crematogaster ants: host distribution rather than adaptation towards specific hosts drives the process. In: Glaubrecht, M (ed.) *Evolution in Action*. Berlin Heidelberg: Springer, pp. 193–213.
- Fernandes, D. N. and Sanford, R. L. (1995). Effects of recent land-use practices on soil nutrients and succession under tropical wet forest in Costa Rica. *Conservation Biology*, 9, 915–922.
- Fisher, B. L. and Zimmerman, J. K. (1988). Ant/orchid associations in the Barro Colorado National Monument, Panama. *Lindleyana*, 3, 12–16.
- Floater, G. J. (1995). Effect of epiphytes on the abundance and species richness of litter-dwelling insects in a Seychelles cloud forest. *Tropical Ecology*, 36, 203–212.
- Fonseca, C. R. (1999). Amazonian ant-plant interactions and the nesting space limitation hypothesis. *Journal of Tropical Ecology*, 15, 807–825.
- Fortuna, M. A. and Bascompte, J. (2006). Habitat loss and the structure of plant–animal mutualistic networks. *Ecology Letters*, 9, 281–286.
- Foster, W. A., Snaddon, J. L., Turner, E. C. et al. (2011). Establishing the evidence base for maintaining biodiversity and ecosystem function in the oil palm landscapes of South East Asia. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366, 3277–3291.
- Frederickson, M. E., Greene, M. J. and Gordon, D. M. (2005). ‘Devil’s gardens’ bedevilled by ants. *Nature*, 437, 495–496.
- Freiberg, M. and Turner, S. M. (2007). Importance of drought on the distribution of the birds nest fern, *Asplenium nidus*, in the canopy of a lowland tropical rainforest in north-eastern Australia. *Austral Ecology*, 32, 70–76.
- Gay, H. and Hensen, R. (1992). Ant specificity and behaviour in mutualisms with epiphytes: the case of Lecanopteris (Polypodiaceae). *Biological Journal of the Linnean Society*, 47, 261–284.

- Gibernau, M., Orivel, J., Delabie, J. H. C., Barabe, D. and Dejean, A. (2007). An asymmetrical relationship between an arboreal ponerine ant and a trash-basket epiphyte (Araceae). *Biological Journal of the Linnean Society*, 91, 341–346.
- Gibson, L., Lee, T. M., Lian Pin Koh et al. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, 478, 378–381.
- Haddad, N. M., Brudvig, L. A., Clobert, J. et al. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, 1, e1500052.
- Hardwick, S. R., Toumi, R., Pfeifer, M. et al. (2015). The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: Forest disturbance drives changes in microclimate. *Agricultural and Forest Meteorology*, 201, 187–195.
- Hodgkison, R., Balding, S. T., Akbar, Z. and Kunz, T. H. (2003). Roosting ecology and social organization of the spotted-winged fruit bat, *Balionycteris maculata* (Chiroptera: Pteropodidae), in a Malaysian lowland dipterocarp forest. *Journal of Tropical Ecology*, 19, 667–676.
- Holtum, R. E. (1976). *Asplenium* Linn., sect. *Thamnopteris* Presl. *Gardens' Bulletin, Singapore*, 27, 143–154.
- Huxley, C. R. (1978). The ant-plants *Myrmecodia* and *Hydnophytum* (Rubiaceae), and the relationships between their morphology, ant occupants, physiology and ecology. *New Phytologist*, 80, 213–268.
- Kaiser-Bunbury, C. N. and Blüthgen, N. (2015). Integrating network ecology with applied conservation: a synthesis and guide to implementation. *AoB Plants*, 7: plv076. doi:10.1093/aobpla/plv076
- Karasawa, S. and Hijii, N. (2006a). Determinants of litter accumulation and the abundance of litter-associated microarthropods in bird's nest ferns (*Asplenium nidus* complex) in the forest of Yambaru on Okinawa Island, southern Japan. *Journal of Forest Research*, 11, 313–318.
- (2006b). Does the existence of bird's nest ferns enhance the diversity of oribatid (Acari: Oribatida) communities in a subtropical forest? *Biodiversity and Conservation*, 15, 4533–4553.
- (2006c). Effects of distribution and structural traits of bird's nest ferns (*Asplenium nidus*) on oribatid (Acari: Oribatida) communities in a subtropical Japanese forest. *Journal of Tropical Ecology*, 22, 213–222.
- King, J. R. and Tschinkel, W. R. (2008). Experimental evidence that human impacts drive fire ant invasions and ecological change. *Proceeding of the National Academy of Sciences*, 105, 20339–20343.
- Klimes, P., Idigel, C., Rimandai, M. et al. (2012). Why are there more arboreal ant species in primary than secondary tropical forests? *Journal of Animal Ecology*, 81, 1103–1112.
- Laughlin, D. C. and Messier, J. (2015). Fitness of multidimensional phenotypes in dynamic adaptive landscapes. *Trends in Ecology & Evolution*, 30, 487–496.
- Laurance, W. F., Camargo, J. L. C., Luizão, R. C. C. et al. (2011). The fate of Amazonian forest fragments: a 32-year investigation. *Biological Conservation*, 144, 56–67.
- Lowe, S., Browne, M., Boudjelas, S. and De Poorter, M. (2000). *100 of the World's Worst Invasive Alien Species: A Selection from the Global Invasive Species Database*. The Invasive Species Specialist Group (ISSG), Auckland, New Zealand, 12 pp.
- Mayer, V. E., Frederickson, M. E., McKey, D. and Blatrix, R. (2014). Current issues in the evolutionary ecology of ant-plant symbioses. *New Phytologist*, 202, 749–764.
- Mikissa, J. B., Jeffery, K., Fresneau, D. and Mercier, J. L. (2013). Impact of an invasive alien ant, *Wasmannia auropunctata* Roger, on a specialised plant–ant mutualism, *Barteria*

- fistulosa Mast. and Tetraponera aethiops F. Smith., in a Gabon forest. *Ecological Entomology*, 38, 580–584.
- Murase, K., Itioka, T., Nomura, M. and Yamane, S. (2003). Intraspecific variation in the status of ant symbiosis on a myrmecophyte, *Macaranga bancana*, between primary and secondary forests in Borneo. *Population Ecology*, 45, 221–226.
- Murase, K., Yamane, S., Itino, T. and Itioka, T. (2010). Multiple factors maintaining high species-specificity in *Macaranga-Crematogaster* (Hymenoptera: Formicidae) myrmecophytism: higher mortality in mismatched ant-seedling pairs. *Sociobiology*, 55, 883–898.
- Ness, J. and Bronstein, J. (2004). The effects of invasive ants on prospective ant mutualists. *Biological Invasions*, 6, 445–461.
- Owusu-Sekyere, E., Cobbina, J. and Wakatsuki, T. (2006). Nutrient cycling in primary, secondary forests and cocoa plantation in the Ashanti Region, Ghana. *West African Journal of Applied Ecology*, 9, 1–9. <http://dx.doi.org/10.4314/wajae.v9i1.45680>
- Padmawathe, R., Qureshi, Q. and Rawat, G. S. (2004). Effects of selective logging on vascular epiphyte diversity in a moist lowland forest of Eastern Himalaya, India. *Biological Conservation*, 119, 81–92.
- Palmer, T. M., Stanton, M. L., Young, T. P. et al. (2008). Breakdown of an ant-plant mutualism follows the loss of large herbivores from an African Savanna. *Science*, 319, 192–195.
- Passmore, H. A., Bruna, E. M., Heredia, S. M. and Vasconcelos, H. L. (2012). Resilient networks of ant-plant mutualists in Amazonian forest fragments. *PLoS ONE*, 7, e40803.
- Patra, B., Bera, S. and Hickey, R. J. (2008). Soral crypsis: protective mimicry of a coccid on an Indian fern. *Journal of Integrative Plant Biology*, 50, 653–658.
- Picard, N., Gourlet-Fleury, S. and Forni, É. (2012). Estimating damage from selective logging and implications for tropical forest management. *Canadian Journal of Forest Research*, 42, 605–613.
- Plowman, N. S., Hood, A. S. C., Moses, J., Redmond, C., Novotny, V., Klimes, P. and Fayle, T. M. (2017). Network reorganization and breakdown of an ant-plant protection mutualism with elevation. *Proceedings of the Royal Society B: Biological Sciences* 284: 20162564. <http://dx.doi.org/10.1098/rspb.2016.2564>.
- Putz, F. E. and Holbrook, N. M. (1988). Further observations on the dissolution of mutualism between *Cecropia* and its ants: the Malaysian case. *Oikos*, 53, 121–125.
- Richardson, B. A., Borges, S. and Richardson, M. J. (2006). Differences between epigeic earthworm populations in tank bromeliads from Puerto Rico and Dominica. *Caribbean Journal of Science*, 42, 380–385.
- Rico-Gray, V. and Oliveira, P. S. (2007). *The Ecology and Evolution of Ant-Plant Interactions*. Chicago: University of Chicago Press.
- Rodgers, D. J. and Kitching, R. L. (1998). Vertical stratification of rainforest collembolan (Collembola: Insecta) assemblages: description of ecological patterns and hypotheses concerning their generation. *Ecography*, 21, 392–400.
- (2011). Rainforest Collembola and the insularity of epiphyte microhabitats. *Insect Conservation and Diversity*, 4, 99–106.
- Rodríguez-Castañeda, G., Forkner, R. E., Tepe, E. J., Gentry, G. L. and Dyer, L. A. (2011). Weighing defensive and nutritive roles of ant mutualists across a tropical altitudinal gradient. *Biotropica*, 43, 343–350.
- Roland, L.-A. R. d., Rabearivony, J., Razafimanjato, G., Robenarimangason, H. and Thorstrom, R. (2005). Breeding biology and diet of Banded Kestrels *Falco zoniventris* on Masoala Peninsula, Madagascar. *Ostrich*, 76, 32–36.

- Sala, O. E., Stuart Chapin, F., III et al. (2000). Global biodiversity scenarios for the year 2100. *Science*, 287, 1770–1774.
- Scheffers, B. R., Edwards, D. P., Diesmos, A., Williams, S. E. and Evans, T. A. (2013). Microhabitats reduce animal's exposure to climate extremes. *Global Change Biology*, n/a-n/a.
- Scheffers, B. R., Phillips, B. L. and Shoo, L. P. (2014). Asplenium bird's nest ferns in rainforest canopies are climate-contingent refuges for frogs. *Global Ecology and Conservation*, 2, 37–46.
- Slik, F. J. W., Keßler, P. J. A. and Welzen, P. C. v. (2003). Macaranga and Mallotus species (Euphorbiaceae) as indicators for disturbance in the mixed lowland dipterocarp forest of East Kalimantan (Indonesia). *Ecological Indicators*, 2, 311–324.
- Snaddon, J. L., Turner, E. C., Fayle, T. M. et al. (2012). Biodiversity hanging by a thread: the importance of fungal-litter trapping systems in tropical rainforests. *Biology Letters*, 8, 397–400.
- Stuntz, S., Ziegler, C., Simon, U. and Zotz, G. (2002). Diversity and structure of the arthropod fauna within three canopy epiphyte species in central Panama. *Journal of Tropical Ecology*, 18, 161–176.
- Talaga, S., Dézerald, O., Carteron, A. et al. (2015). Tank bromeliads as natural microcosms: a facultative association with ants influences the aquatic invertebrate community structure. *C. R. Biol.*, 338, 696–700.
- Tanaka, H., Inui, Y. and Itioka, T. (2009). Anti-herbivore effects of an ant species, *Crematogaster difformis*, inhabiting myrmecophytic epiphytes in the canopy of a tropical lowland rainforest in Borneo. *Ecol. Res.*, 24, 1393–1397.
- Tanaka, H. O., Yamane, S., Nakashizuka, T., Momose, K. and Itioka, T. (2007). Effects of deforestation on mutualistic interactions of ants with plants and hemipterans in tropical rainforest of Borneo. *Asian Myrmecology*, 1, 31–50.
- Thorstrom, R. and Roland, L.-A. R. d. (2000). First nest description, breeding behaviour and distribution of the Madagascar Serpent-Eagle *Eutriorchis astur*. *Ibis*, 142, 217–224.
- Tilman, D., Fargione, J., Wolff, B. et al. (2001). Forecasting agriculturally driven global environmental change. *Science*, 292, 281–284.
- Turner, E. C. (2005). The ecology of the Bird's Nest Fern (*Asplenium* spp.) in unlogged and managed habitats in Sabah, Malaysia. PhD, University of Cambridge, Cambridge.
- Turner, E. C. and Foster, W. A. (2006). Assessing the influence of Bird's nest ferns (*Asplenium* spp.) on the local microclimate across a range of habitat disturbances in Sabah, Malaysia. *Selbyana*, 27, 195–200.
- (2009). The impact of forest conversion to oil palm on arthropod abundance and biomass in Sabah, Malaysia. *Journal of Tropical Ecology*, 25, 23–30.
- Turner, E. C., Snaddon, J. L., Johnson, H. R. and Foster, W. A. (2007). The impact of bird's nest ferns on stemflow nutrient concentration in a primary rain forest, Sabah, Malaysia. *Journal of Tropical Ecology*, 23, 721–724.
- Tylianakis, J. M., Laliberté, E., Nielsen, A. and Bascompte, J. (2010). Conservation of species interaction networks. *Biological Conservation*, 143, 2270–2279.
- Walter, D. E., Seeman, O., Rodgers, D. and Kitching, R. L. (1998). Mites in the mist: how unique is a rainforest canopy knockdown fauna? *Australian Journal of Ecology*, 23, 501–508.
- Watkins, J. E., Cardelús, C. L. and Mack, M. C. (2008). Ants mediate nitrogen relations of an epiphytic fern. *New Phytologist*, 180, 5–8.

- Weathers, K. C., Cadenasso, M. L. and Pickett, S. T. (2001). Forest edges as nutrient and pollutant concentrators: potential synergisms between fragmentation, forest canopies, and the atmosphere. *Conservation Biology*, 15, 1506–1514.
- Wetterer, J. K. (1997). Ants on *Cecropia* in Hawaii. *Biotropica*, 29, 128–132.
- Wilcove, D. S., Giam, X., Edwards, D. P., Fisher, B. and Koh, L. P. (2013). Navjot’s nightmare revisited: logging, agriculture, and biodiversity in Southeast Asia. *Trends in Ecology & Evolution*, 28, 531–540.
- Yu, D. W., Wilson, H. B. and Pierce, N. E. (2001). An empirical model of species coexistence in a spatially structured environment. *Ecology*, 82, 1761–1771.