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Living together in novel habitats: A review of land-use change impacts on mutualistic ant-plant symbioses in tropical forests

Tom M. Fayle[1,2], Chua Wanji[3], Edgar C. Turner[4] and Kalsum M. Yusah[3]

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[1]Institute of Entomology, Biology Centre of Academy of Sciences Czech Republic, and Faculty of Science, University of South Bohemia, Branisovska 31, 37005, Ceske Budejovice, Czech Republic

[2]Forest Ecology and Conservation Group, Imperial College London, Silwood Park Campus, Buckhurst Road, Berkshire, SL5 7PY, UK

[3]Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, 88400, Kota Kinabalu, Sabah, Malaysia

[4]Insect Ecology Group, University Museum of Zoology Cambridge, Downing Street, Cambridge, CB2 3EJ, UK

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, $C0_2$ 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).

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 is moderately well-known, changes in species interaction networks are much less-studied, yet also 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 re-growth, 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.

[Figure 3.1 here]

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 increase in abundance following burning of pasture (anecdotal report; Fonseca, 1999). It is worth noting that these 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 specialise 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 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 to 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 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 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 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 only survive 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 below). 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 only be extrapolated 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. In review). 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 domatia of the tree *Barteria fistulosa* in secondary forests in Gabon, and consequently reducing occupation by the native ant *Tetraponera 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.

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 the 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 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; Karasawa & Hijii, 2006c; Karasawa & Hijii, 2006b; Karasawa & Hijii, 2006a; 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 decomposition of leaf litter (Snaddon *et al.*, 2012) are also found in 36% of the ferns in the litter held in the fern rosette (30 of the 83 ferns from Fayle *et al.* (2012)).

[Figure 3.2 here]

The most abundant animal group found in bird's nest ferns are the ants, comprising on average 86% of individuals, and 91% 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 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 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 (Bluthgen *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 each other for nesting space within the ferns, 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%) 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 (http://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).

[Figure 3.3 here]

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% decrease) and biomass (87.5% decrease) between ferns in primary forest and those in oil palm plantation (Turner & Foster, 2009), the numbers of species of ants per fern does 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 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 fern size and 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 3.3a). 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 3.3b), causing in 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.

[Figure 3.4 here]

Future research directions

As the review above 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 3.3. and also 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 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.

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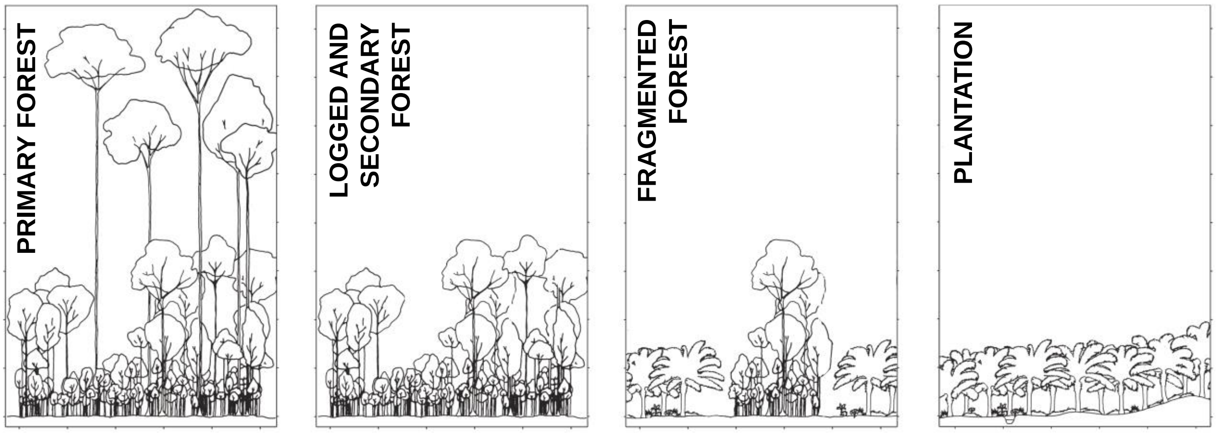

Figure 3.1 Typical habitat conversion gradient for tropical forests. Note that there are two categories of continuous non-primary forest, combined here for brevity: logged forest, which is primary forest with timber selectively extracted, and secondary regrowth forest, which has regenerated following 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.

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 Chi'en Lee; inset Tom Fayle.

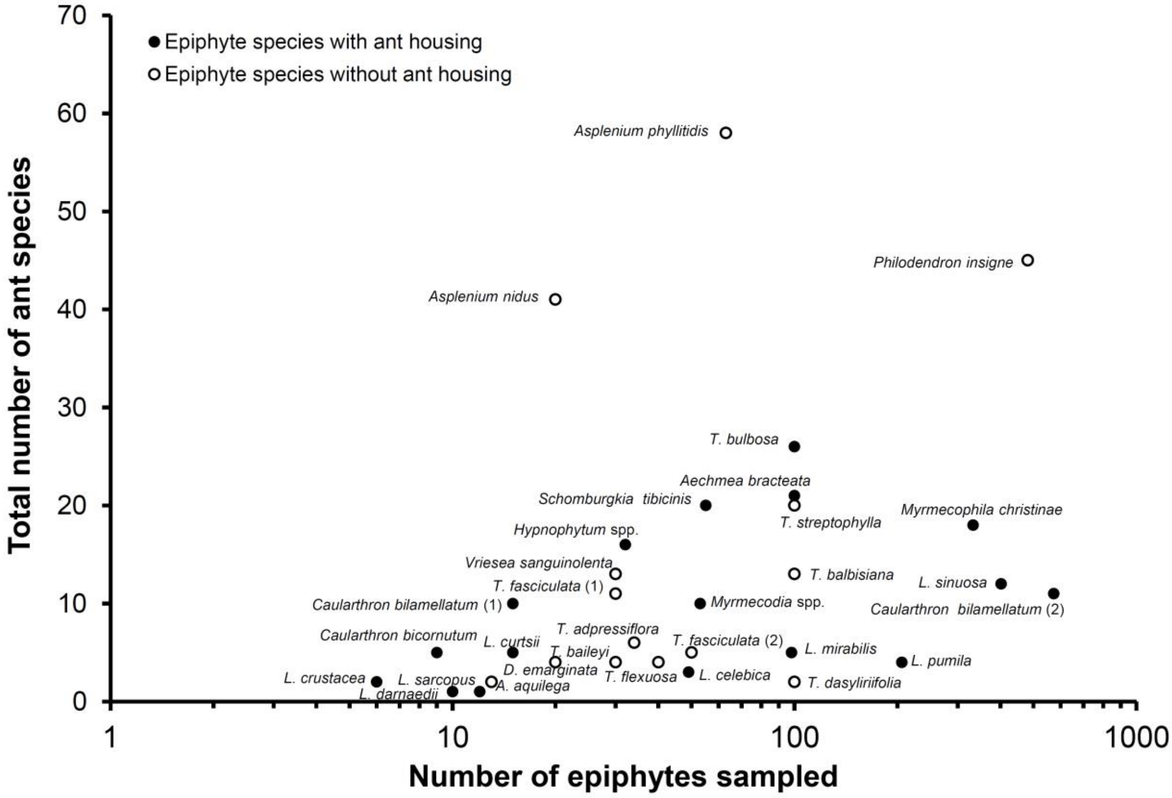

Figure 3.3. Number of different symbiotic ant species found inhabiting epiphytes plotted in relation to sampling intensity and presence of ant housing. Some genus names are abbreviated for clarity: *Tillandisa*, *Leucanopteris*, *Dimerandra*, *Aechmea*. Two species are represented twice, denoted numerically 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).

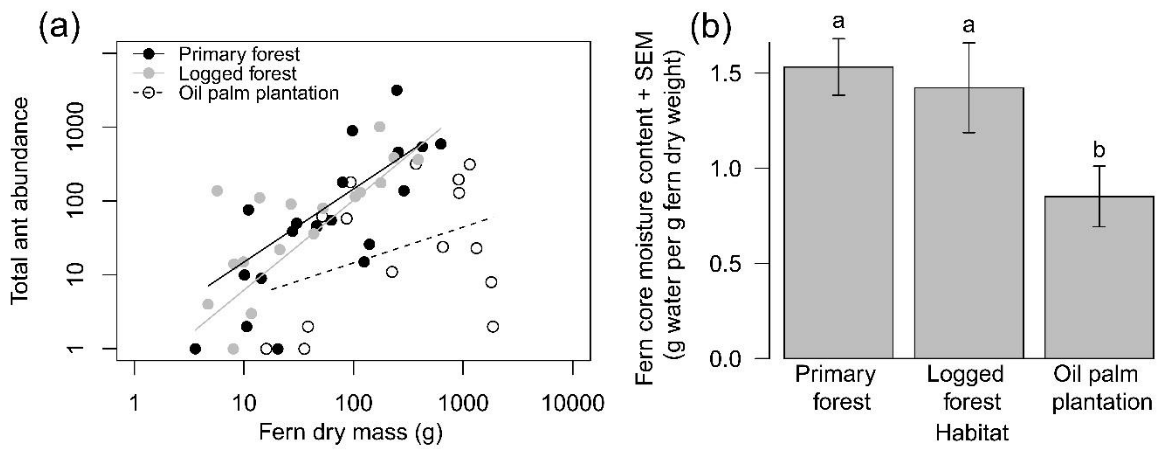

Figure 3.4. (a) The volume of suitable nesting space for ants in ferns differs between habitats, with ferns in oil palm plantation supporting lower total abundances of ants per unit dry weight than ferns from forest habitats. (b) One explanation for this is that ferns in oil palm plantations have significantly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

Table 3.1. Summary of known impacts of human-driven habitat change on ant-plant symbiotic networks. *the 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. **and nearby areas.

Habitat change type	Plant taxa	Ant taxa	Location	Habitat(s)	Habitat change	Main conclusions	Reference(s)
Logging or forest clearance with regrowth	*Teijsmanniodendron, Horsefieldia, Ficus, Macaranga*	*Anonychomyrma, Camponotus*	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)
	Asplenium nidus, A. phyllitidis	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)
	Macaranga bancana	*Crematogaster* spp.	Malaysian Borneo	Lowland rain forest	Conversion to secondary forest*, cultivated land or grassland	More saplings inhabited by non-partner *Crematogaster* species in secondary forest than primary forest.	Murase et al (2003)
	Cecropia	*Azteca*	Brazilian Amazon	Pasture	Regrowth following burning and abandonment of pasture	Anecdotal account of forest regeneration, with *Cecropia* ant-plants dominant. Initially many, small ant-plants, with later thinning out as plants grow. *Cecropia* dominate the overstory for > 10 years, and are then replaced by later succession trees.	Fonseca (1999)
Forest fragmentation	*Hirtella*, many others	*Allomerus, Azteca*, 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)
	Hirtella, Maietia, many others	*Allomerus, Pheidole*, 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)
Clearance for agriculture	*Myrmecodia, Hydnophytum*	*Iridomyrmex*, 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 *Myrmecodia* in undisturbed lowlands, opposite for *Hydnophytum*. More species of ant in *Myrmecodia* in disturbed highlands, very few species of ant in *Hydophytum* in highlands (note: as very small number of species, no formal analyses conducted).	Huxley (1978)
	Asplenium nidus, A. phyllitidis	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)
	Hohenbergia, Aechmea	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)