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Biodiversity, species interactions, and functional roles of ants (Hymenoptera: Formicidae) in fragmented landscapes: a review

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Abstract

Ants play a central role in understanding the effects of habitat loss and fragmentation on communities and ecosystems because of their diversity, abundance, and functional roles in ecosystems. Species interactions involving ants are widespread and include other insects, plants, and vertebrates. Ants often do not show strong relationships between species richness and habitat area, but shifts in ant species composition are a more general pattern with an average 75% turnover in species composition among habitat fragments. Shifts in ant species composition and relative abundance due to habitat fragmentation have direct and indirect effects on species interactions of ants, including sap-feeding insects, seed dispersal, and vertebrate mutualisms. The loss of some ant species from small habitat fragments may have widespread effects in ecosystems because of their function roles as keystone mutualists or in soil modification. Boundary dynamics of ants across habitat edges and the surrounding land uses are particularly important to understanding the effects of habitat fragmentation because steep abiotic and biotic gradients may facilitate invasive ant species and cause sharp changes in the abundance and species interactions of native ant species.

Key words: Ecosystem function, edge effects, functional groups, habitat fragmentation, invasive species, landscape ecology, mutualisms, review, soils.

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Introduction

The loss and fragmentation of natural habitats have altered biodiversity at local, regional, and global scales. At local scales, a decrease in the size of habitat remnants often leads to a reduction in species richness consistent with the well known species-area relationships, while the effects of increased fragmentation are more variable (FAHRIG 2003). Agricultural or urban land uses in the surrounding areas also influence the species composition within habitat remnants through edge effects or the establishment of invasive species (EWERS & DIDHAM 2005, CROWL & al. 2008, LINDENMAYER & al. 2008). At the regional scale, habitat patches isolated by land use may differ substantially in species composition because of species aggregation, dispersal limitation, or chance effects of colonization and extinction (LEIBOLD & al. 2004, TSCHARNTKE & al. 2007). At the global scale, biotic homogenization and climate-change effects are predicted to reduce the size of regional species pools (CHAPIN & al. 2000, DAVIS 2003).

A growing body of evidence suggests that the loss of biodiversity can alter ecosystem functions and services that are important to sustaining natural and human-managed ecosystems (CHAPIN & al. 2000, CHAPMAN & BOURKE 2001, PETCHEY & GASTON 2006). Recent attention to the relationships between biodiversity and ecosystem function has heightened awareness of the role of invertebrate diversity in the loss of ecosystem functions. This is particularly true of the ants (FOLGARAIT 1998), which are increasingly viewed as a focal taxon for ecosystem monitoring land management and conservation (BESTELMEYER & WIENS 2001, ANDERSEN & MAJER 2004, UNDERWOOD & FISHER 2006, MAJER & al. 2007, RÍOS-CASANOVA & BESTELMEYER 2008).

The groundswell interest in ants as bioindicators of ecosystem dynamics stems from the recognition that ant communities respond to ecosystem disturbance, and therefore ants became an integral part of monitoring faunal changes with mine restoration, grazing by livestock, or agricultural practices (MAJER 1983, ANDERSEN 1990, BESTELMEYER & WIENS 1996, 2001, WHITFORD & al. 1999, PERFECTO & VANDERMEER 2002, ANDERSEN & MAJER 2004). Now, ants are becoming widely used in ecosystem monitoring for a wide range of land-use effects and, more recently, to examine invertebrate responses to habitat fragmentation. Two recent reviews (ANDERSEN & MAJER 2004, MAJER & al. 2007) synthesize the major finds of ants as bioindicators of changes in the abiotic environment and the responses of plants and animals in ecosystem restoration. The findings and methodological issues from studies of ants in the broader context of conservation monitoring were reviewed by ANDERSEN & MAJER (2004) and UNDERWOOD & FISHER (2006). Here, I focus on ant responses to habitat loss, fragmentation, and the surrounding land use at levels of organization including communities, functional groups, and individual species. I also consider how the loss and fragmentation of natural habitat influence species interactions and food-web dynamics of ants, and how these are important to biodiversity conservation.

A literature search in the Web of Science (ISI 2008) using the key words "ants" and "habitat fragmentation" yielded a total of 75 studies that examined some aspect of ant species and community responses to habitat loss and fragmentation. In the past 15 years, there was a steady increase in the number of published papers each year and an exponential growth in the number of citations of fragmentation studies on ants (Fig. 1). Studies on the use of ants in conservation monitoring for habitat loss and fragmentation are more recent (largely since 2000; Fig. 1) than the broader interest in monitoring ant biodiversity, which dates back to the 1980s (MAJER & al. 2007).

Overview of ant responses to habitat loss and fragmentation

Habitat loss refers to the reduction in area of natural habitat, whereas fragmentation is a decrease in the connectivity of habitat (FAHRIG 2003). Although both processes operate simultaneously during land-use change, the distinction between area and fragmentation per se can be useful since the distribution of ant species may vary with habitat area, isolation, edge effects, and surrounding land uses (Fig. 2). As habitat area decreases, edge habitat becomes proportionately larger and interior habitat smaller. Therefore, differences in ant species richness and composition between habitat fragments and the surrounding matrix should be greater for large fragments than for small ones. Likewise, for fragments of a given area, differences in ant species composition between the fragment and the surrounding matrix should increase with land-use intensity or the degree of boundary contrast in the abiotic and biotic environments between fragments and the surrounding matrix (Fig. 2). In landscapes with numerous small habitat fragments, community composition within fragments might be largely controlled by land-use practices in the surrounding matrix. Fragmentation increases isolation between patches, resulting in lower dispersal and colonization of suitable habitats and the potential for greater influences of surrounding land uses (Fig. 2). The loss and fragmentation of natural habitat, and its concomitant replacement by intensive land uses, may cause substantial shifts in ant communities by changing abiotic conditions, the availability of food and nest sites, and the abundance of mutualists or competitors. Increased edge habitat in fragmented landscapes may facilitate invasions by non-native ant species, which may alter the composition of native ant communities (Fig. 2).

Shifts in functional group composition also occur in the abiotic and biotic changes with habitat loss and fragmentation. Increased solar insolation in the surrounding land use and along habitat edges favors dominant dolichoderine species, whereas generalized myrmicines and opportunists may be negatively affected by a loss of canopy cover and increased solar radiation (HOLWAY & al. 2002a, ANDERSEN & MAJER 2004). These shifts in functional group abundance due to the abiotic environment alter the outcome of interspecific encounters among ants, which favor shifts from aggressive dolichoderines to subdominant and opportunistic myrmicines or climate specialists (BESTELMEYER & WIENS 1996, ANDERSEN & MAJER 2004).

At the level of individual species, changes in distribution and abundance in fragmented landscapes can have a variety of consequences for species interactions. A reduction in the abundance of *Aphaenogaster* spp. in forest fragments in eastern North America, for example, results in decreased seed dispersal of elaiosome-bearing understory plants. Several other types of species ant-plant, ant-hemipteran, ant-bird interactions may be altered by habitat loss and fragmentation (Fig. 2). Examples of these are considered in more detail below.

Community and functional group responses

Species richness: The species-area relationship has been a mainstay of describing community changes to habitat loss in fragmented landscapes (WATLING & DONNELLY 2006). Surprisingly, however, ant communities often do not show strong relationships between habitat area and species richness. Of six studies that reported data on relationships between ant species richness and habitat area, four showed no statistically significant relationship (ABENSPERG-TRAUN & al. 1996, ARMBRECHT & ULLOA-CHACON 2003, MAETO & SATO 2004, DAUBER & al. 2006). VASCONCELOS & al. (2006) reported a significant species-area relationship for ants in forest fragments in the Amazon rainforest, but most of the variation in species richness was unexplained. In contrast, SUAREZ & al. (1998) found a strong effect of habitat area on ant species richness in native coastal scrub of southern California. The species-area relationship, however, was highly contingent on the presence of the invasive Argentine ant, *Linepithema humile* (MAYR, 1868), which uniformly lowered ant species richness compared to uninvaded fragments of similar size. Fragments invaded by *L. humile* were later shown to be in mesic canyons whereas uninvaded fragments were on xeric hilltops (HOLWAY & al. 2002a). SCHOEREDER & al. (2004) documented a strong species-area relationship ($r^2 = 0.94$ for a power-function regression of species richness on habitat area) for ant communities in Atlantic tropical rainforest fragments in southeastern Brazil. At a finer scale, GOLDEN & CRIST (2000) experimentally manipulated patch sizes (1 - 16 m^2) of old-field vegetation in the eastern US and found no area effects on ant species richness, but richness varied consistently with the amount of habitat edge. ZSCHOKKE & al. (2000) recorded increases of ant species richness over a similar range of patch areas in experimental patches within calcareous grasslands in Switzerland, but patch-area effects on ant richness did not differ among fragmented and unfragmented patches. GIBB & HOCHULI (2002) reported significantly higher species richness of ants in small urban fragments of eucalyptus forest than in large continuous forests in nearby parks, primarily due to the increased species richness of generalized myrmicine and opportunistic ants. Based on these few data sets, there is no consistent pattern in the predictability of species-area effects across data sets that differ in spatial scale (1 m^2 - 500 ha), habitat type (grassland, shrubland, temperate or tropical forest) or the overall species richness of the ant community (13 - 268 species).

Two studies suggest that present-day or historical connectivity of habitat fragments affects ant species richness. ABENSPERG-TRAUN & al. (1996) found that overall ant species richness was greater in fragments of eucalyptus forest that were connected by strips of native vegetation in Western Australia. SUAREZ & al. (1998) documented a

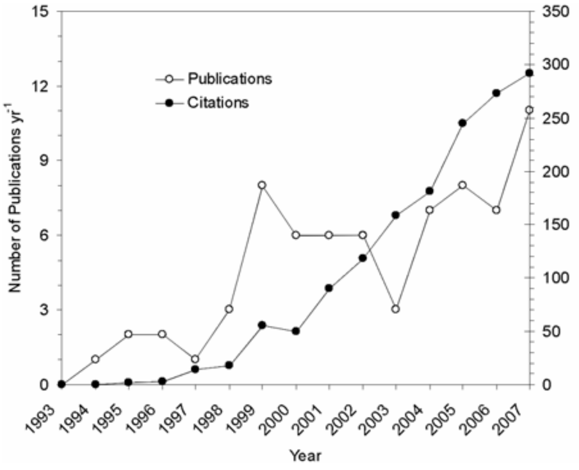

Fig. 1: Growth in the number of studies published and cited on ants and habitat fragmentation from 1993 - 2007.

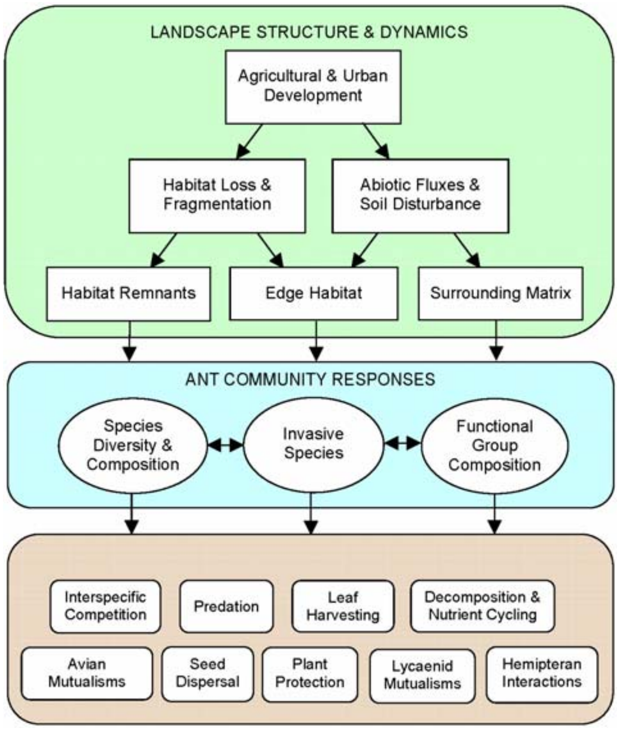

Fig. 2: Conceptual framework for the effects of habitat loss and fragmentation on ant community diversity and composition, functional groups, and species interactions.

negative relationship between ant species richness and time since fragment isolation, suggesting that few recolonizations occur following local extinctions in isolated habitats. In contrast, Vasconcelos & al. (2006) found no effect of isolation of forest fragments on ant species richness, perhaps because most fragments were < 300 m apart. Isolation distances of 1 - 3 km between habitats may be sufficient to limit queen dispersal for several ant species, based on levels of genetic differentiation among ant populations (Seppä 2008).

The structure of the intervening matrix may also influence ant species richness in fragmented landscapes. Perfecto & Vandermeer (2002) showed that ant species richness in shade-coffee agroecosystems in southwestern Mexico was similar to that in adjacent native montane forests, whereas more intensively managed sun-coffee farms were significantly lower in ant richness. Edge effects on species richness between native forest and sun-coffee farms were also more pronounced than with shade coffee. The shade-coffee systems therefore provided more suitable matrix for native ants, and could serve to increase the connectivity of ant communities between forest habitats (Perfecto & Vandermeer 2002). In an Afromontane forest-grassland mosaic, ant species richness was similar across forest-grassland edges and both habitats contributed to the regional ant richness, even though grasslands are viewed as having lower conservation value than forest remnants (Kotze & Samways 2001). These examples serve to illustrate that a dichotomous habitat-matrix view may have limited value in understanding community responses to habitat fragmentation, especially where the surrounding matrix is characterized by low-intensity land use. High levels of boundary contrast between cultivated fields and natural meadows in an agricultural landscape of central Germany resulted in different ant species richness and composition along field edges (Dauber & Wolters 2004).

Species composition: A more general pattern from fragmentation studies of ant communities is a shift in ant species composition with habitat area, heterogeneity, or edge effects. In contrast to area effects on species richness, studies consistently show pronounced shifts in ant species composition across a gradient of habitat areas. Gibb & Hochuli (2002) noted considerable turnover in ant community composition between large and small woodland fragments that, in part, could be explained by shifts in functional group composition. Dauber & al. (2006) recorded comparable levels of similarity (30 - 40%) in ant species composition among fragments of large and small size classes; shifts in species composition were attributed to variation in vegetation cover and grazing. In their experimental study of calcareous grasslands, Zschokke & al. (2000) found that ant species dissimilarity was greater among locations than across area or fragmentation treatments within locations. This suggests that spatial effects such as dispersal limitation or intraspecific aggregation within preferred habitat patches may lead to species sorting of ants among habitat fragments.

Two recent studies emphasize shifts in ant species composition among habitat fragments using multivariate variance partitioning of the effects of habitat area, heterogeneity and the surrounding land uses. Debuse & al. (2007) decomposed the effects of habitat area and heterogeneity on ant community composition from fragmented *Eucalyptus* woodlands in southeastern Australia. Although patch area was the single most important variable to influence species composition (11% of the variation), soil clay content, rainfall, and disturbance together comprised most of the variation (24%) in species composition (Debuse & al. 2007). Using a similar approach, Spiesman & Cumming (2008) partitioned the variation in ant species composition in native fragments of sandhill habitat in northern Florida, USA. Interestingly, however, the surrounding land uses (pine plantation and urban) had a greater influence on species composition than the area of the native sandhill habitat because generalist ant species replaced specialists in fragments surrounded by other land uses (Spiesman & Cumming 2008). At broader scales, spatial effects also explained more of the variation in species composition among ant communities (27%) than habitat area and heterogeneity (22%), suggesting that colonization-extinction dynamics and dispersal limitation play an important role in structuring ant communities in fragmented habitats.

Edge effects and invasive species: Ant species distributions vary in a complex manner across boundaries between habitat fragments and surrounding land uses. Edge effects on ant species composition arise due to sharp gradients in abiotic conditions, disturbance, or the presence of invasive species. These processes are reflected in shifts in functional group composition: greater abundances of dominant dolichoderines and hot climate specialists in surrounding land uses and in edge habitats to higher abundances of generalized myrmicines and cryptic species, and cold climate specialists within natural habitat fragments (DEBUSE & al. 2007). Spillover may also occur across habitat edges, in which colony establishment in habitat fragments is subsidized by source populations in the surrounding land use (or vice versa). DAUBER & al. (2006) found little evidence for spillover effects in grassland remnants in Sweden, however, perhaps because few ant species occurred in the surrounding agricultural matrix.

One of the best-studied cases is the invasive Argentine ant, *Linepithema humile*, which shows a monotonic decline in abundance from urban edges to the interior of coast habitat scrub in southern California, USA (SUAREZ & al. 1998, HOLWAY & al. 2002a, BOLGER 2007). Higher abundance near edges likely stems from spillover between urban sources into habitat fragments (BOLGER 2007). Steeper gradients in abundance of *L. humile* occur in mesic canyons than in xeric hilltops because colony survival is greater in environments with higher moisture, whereas native ants were more tolerant of dry conditions (HOLWAY & al. 2002a). These differences in environmental tolerance create a competitive advantage of *L. humile* over native species along urban edges of mesic fragments. This results in very different species richness and composition of native ants in habitat edges of xeric and mesic remnants (HOLWAY & al. 2002a). ARMBRECHT & ULLOA-CHACON (2003) reported lower native ant species richness in dry-forest remnants of Colombia that were invaded by the little fire ant, *Wasmannia auropunctata* (ROGER, 1863). There was a consistent decline in native ant species richness with increased abundance of *W. auropunctata*, which appeared to be related to land-use intensity and disturbance in the surrounding matrix (ARMBRECHT & ULLOA-CHACON 2003).

More generally, invasive ant species may exert community-wide influences on ant species richness and composition through a variety of mechanisms involving interference and exploitative competition (HOLWAY & al. 2002b). *Linepithema humile* affects native ants in edge habitats through physical aggression by workers as well as more efficient exploitation of food resources (HUMAN & GORDON 1996, HOLWAY 1999). *Wasmannia auropunctata* shows similar patterns of interference, exploitation, and displacement with native ants (CLARK & al. 1982, HOLWAY & al. 2002b). Likewise, the red imported fire ant, *Solenopsis invicta* BUREN, 1972, is competitively dominant among ant assemblages in disturbed environments (WOJCIK 2001, HOLWAY & al. 2002b). *Solenopsis invicta* does not negatively affect native ant communities in intact native upland remnants in north-central Florida, however, suggesting that competitive dominance occurs largely in disturbed habitats rather than in native habitat remnants (KING & PORTER 2007). These and other examples (HOLWAY & al. 2002b) support the hypothesis that habitat fragmentation and disturbance facilitates community invasion and competitive dominance by invasive ants in a wide range of ecosystems. Invasive ants appear to have a less important role in structuring native ant communities in the interiors of larger habitats with lower levels of anthropogenic disturbance.

To summarize, the effects of habitat loss and fragmentation on ant species diversity and community composition involve a wide range of processes that depend on habitat area, disturbance, edge dynamics, and invasive species. Changes in ant species richness with habitat area and fragmentation are variable, whereas pronounced shifts in species composition often occur, as individual species differ in abundance or occurrence among habitat fragments.

Integration of species richness and composition: One way to link species richness to shifts in species composition is through additive partitions of diversity (VEECH & al. 2002, CRIST & VEECH 2006). In additive partitions of species richness, α is the average number of species within a habitat and β is the difference in species present among habitats. The β-component can be viewed as the average number of species that are absent in a given fragment but present somewhere else in the landscape (VEECH & al. 2002, CRIST & VEECH 2006). These two components are related as $\alpha + \beta = \gamma$, where γ is the total number of species recorded across the entire set of habitats (LANDE 1996). I calculated the α- and β-components of species richness within and among habitat remnants from 11 studies (see Appendix, as digital supplementary material to this article, at the journal's web pages) that sampled a minimum of 10 habitat fragments and that provided the necessary data. When α and β are expressed as a function of γ, a very general relationship emerges across studies (Fig. 3). The α- and β-components of ant species richness as a proportion of γ were remarkably consistent across the 11 studies with very different total richness (γ = 13 - 268 species), such that the slopes for α and β are 0.25 and 0.75 of the total γ (r^2 = 0.89 and 0.99, respectively). Thus, in a set of isolated habitat fragments, 25% of total sampled richness resides within a fragment, and 75% of the total richness occurs through shifts in species distributions among fragments. These relationships quantify the relative importance of species richness and composition in studies of habitat loss and fragmentation. The generality of this result is surprising, given that these studies span tropical and temperate environments and include both small-scale experiments and broad-scale landscape studies (habitat areas 1 m^2 - 500 ha). Elsewhere, CRIST & VEECH (2006) demonstrated that for a given species pool (γ), the α-component of species richness varies primarily with sample grain (i.e., habitat area), whereas the β-component varies with spatial extent (i.e., landscape area). Therefore, with an increasingly large species pool or spatial extent, β becomes an increasingly large component of γ in terms of absolute species richness.

Ant species interactions and functional roles in ecosystems

The complex suite of changes in ant species diversity and composition may have wide ranging effects on species

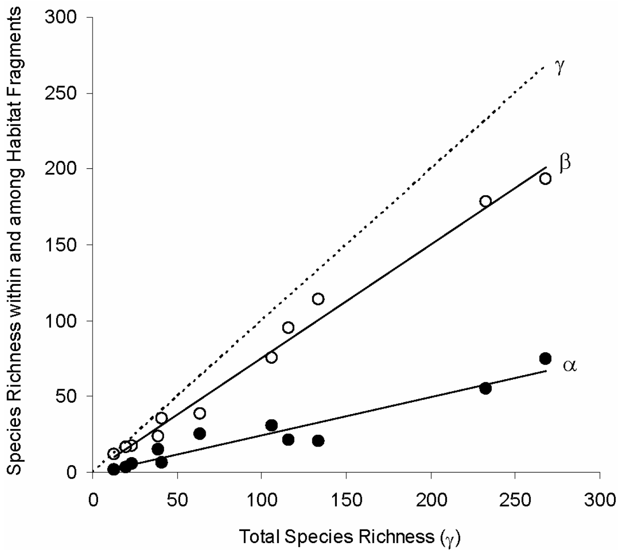

Fig. 3: Patterns of ant species diversity and composition within (α) and among (β) habitat fragments from 11 different studies (for details, see Appendix, as digital supplementary material to this article, at the journal's web pages). The α-component is the average number of species present within a fragment, and the β-component is the average number of species absent from a given fragment. The γ-component is the total number of species across all fragments, and α + β = γ. Across the 11 studies, α and β scale consistently as 0.25 and 0.75 of the total γ, respectively.

interactions, food web dynamics, and functional roles in ecosystems. As noted above, several studies have examined the effects of invasive species on native ant communities in habitat fragments and found evidence for interspecific competition and displacement, or shifts in ant communities due to individualistic responses to altered abiotic conditions. In this section, I consider how changes in ant species composition and abundance with habitat fragmentation may influence other types of species interactions and ecosystem processes.

Ant-aphid interactions: Interactions between ants and aphids are widespread on plants, and the nature of this relationship varies spatially and temporally from mutualistic to antagonistic (Stadler & Dixon 2005). Habitat loss and fragmentation can therefore have an important effect on aphid attendance by ants and the outcome of these interactions, especially in temperate zones where aphid diversity and abundance is greatest (Stadler & Dixon 2005). Since ant species that collect honeydew are primarily in the Formicinae, Dolichoderinae, and, to a lesser extent, the Myrmicinae (Stadler & Dixon 2005), ant-aphid relationships might vary in fragmented habitats with ant functional group shifts in dominant dolichoderines, opportunists, cold-climate specialists and subordinate Camponotini (Andersen & Majer 2004). Changes in host-plant composition with fragmentation and land use may also influence the myrmecophilous (and non-myrmecophilous) aphid species that are available to ants.

In experimentally fragmented grasslands, Braschler & al. (2003) observed greater numbers of aphid colonies of larger size in fragmented than in control plots along with a concomitant increase in the number of ant colonies. Aphid species composition differed in fragmented and control plots despite similar host-plant availability; most aphid species increased in abundance with fragmentation and were attended by ants (Braschler & al. 2003). The most abundant ant species, *Lasius paralienus* Seifert, 1992, was also the most common to attend aphids, but other cold-climate specialists (*Lasius* spp. and *Formica* spp.) and generalized myrmicines (*Myrmica* spp.) attended aphids. A greater ant abundance and aphid attendance in fragmented plots, however, did not reduce predation or parasitism on aphids (Braschler & al. 2003), perhaps because the distribution of natural enemies was also influenced by fragmentation.

Interactions between ants and aphids may extend to other parts of the insect community. Kobayashi & al. (2008) conducted a series of experimental manipulations to show that aphid tending by species of *Lasius*, *Formica*, and *Monomorium* lowered larval survivorship of a nymphalid butterfly, the giant purple emperor, *Sasakia charonda* (Hewitson, 1863), in host hackberry trees (*Celtis* spp.) due to predation by ants on butterfly larvae. Aphid abundance was highest in isolated *Celtis* trees within meadows, intermediate within a small secondary forest, and lowest within large forest patches. Shifts in the relative abundance of four aphid species also occurred across sites. Interestingly, ant abundance in trees reflected changes in aphid density across sites, and different ant species attended aphids in trees: *Lasius sakagamii* Yamauchi & Hayashida, 1970 and *Formica japonica* Motoschoulsky, 1866 primarily occurred in meadows, *Lasius niger* (Linnaeus, 1758) and *Pristomyrmex punctatus* (F. Smith, 1860) [as "*Pristomyrmex pungens* (Mayr, 1866)"] in small secondary forests, and *Monomorium intrudens* F. Smith, 1874 in large forest. Predation on butterfly larvae by ants was highest in trees where aphids were most abundant. Thus, changes in aphid abundance and ant attendance across a gradient of forest patch size indirectly affected ant predation rates on butterfly larvae, which, in this case, is a species of conservation concern (Kobayashi & al. 2008).

Ant-lycaenid interactions: In the previous example, ants acted as predators on butterfly larvae, an interaction that differs from the well studied relationships between ants and the larvae of many butterflies in the family Lycaenidae. Several of the same ant subfamilies (Formicinae, Myrmicinae, Dolichoderinae) and genera (*Lasius*, *Formica*, *Camponotus*, *Crematogaster*, *Myrmica*, *Tapinoma)* that collect honeydew from heteropteran insects or nectar from extrafloral nectarines are also involved in ant-lycaenid interactions and, as with ant-aphid interactions, lycaenid butterfly species vary widely in their degree of obligate or facultative myrmecophily (Pierce & al. 2002, Fiedler 2006). As with ant-aphid interactions, the effects of habitat loss and fragmentation may be particularly complex because habitat alteration may cause shifts in the availability of suitable host plants for myrmecophilous butterflies as well as ant attendants. A particularly interesting case is detailed by Hochberg & al. (1994), who used empirical information to develop a model for understanding how populations of the endangered large blue butterfly, *Maculinea rebeli* (Hirschke, 1904) interact with their gentian host plant (*Gentiana cruciata* Linnaeus) and their obligate ant hosts (*Myrmica* spp.) in the Spanish Pyrenees. Early larval instars of *M. rebeli* feed on host plants. Later instars drop off plants and *Myrmica* workers take them into nests, where they feed the butterfly larvae. If host plants are outside of the foraging range of *Myrmica* nests, then late-instar larvae die before pupating into adults. The model by HOCHBERG & al. (1994) captures the direct and indirect interactions, where butterflies require *Gentiana* plants and *Myrmica* ants but have negative impacts on populations of its host plants and ants. *M. rebeli* population size, in turn, is limited by host-plant and ant-colony densities. Because nest parasitism by *M. rebeli* differentially affects worker production, the butterfly indirectly reduces pre-emptive competition among colonies of different *Myrmica* spp. (HOCHBERG & al. 1994). The effects of habitat loss and fragmentation on butterfly populations therefore depend strongly on changes in the population sizes of host plants and ants.

At a broader spatial scale, NOWICKI & al. (2007) recorded the metapopulation structure of three species of *Maculinea* butterflies in relation to area and connectivity of host-plant patches. All three *Maculinea* spp. showed a positive relationship of occupancy to area of host-plant patches, and two showed a positive effect of connectivity. Within occupied patches, however, butterfly densities were negatively affected by area of host-plant patches and positively influenced by edge effects. The authors attributed higher densities in small patches due to closer proximity of *Myrmica* ant colonies. They hypothesized that higher butterfly abundance in more fragmented patches was due to past parasitism of ant colonies by *Maculinea* within the interiors of host-patches and the spread of *Myrmica* colonies into the edges of plant patches from surrounding areas (NOWICKI & al. 2007). Thus, the complex direct and indirect effects of *Maculinea* spp. on *Myrmica* ant colonies may have a strong spatial component mediated by the boundary dynamics of butterfly larvae and worker movements between host patches and non-host areas.

Ant-myrmecochore interactions: Seed dispersal by ants may be strongly influenced by habitat loss and fragmentation. Several ant genera in four major subfamilies are associated with seed dispersal worldwide through the consumption of lipid-rich elaisomes and subsequent disposal of intact seeds away from parent plants or in microsites favorable for germination (GÓMEZ & ESPADALER 1998). Although the ecological aspects of seed dispersal by ants are well known, few studies have examined how habitat loss and fragmentation may disrupt seed-dispersal mutualisms between ants and plants. MITCHELL & al. (2002) found differences in species composition and relative abundance in a guild of seed-dispersing ants between large and small forest fragments and between large fragments surrounded by high or low land-use intensity in the southern Appalachian mountains, USA. *Aphaenogaster fulva* ROGER, 1863 was dominant at all sites, but decreased in abundance in small fragments; three other species – *Aphaenogaster rudis* J. ENZMANN, 1947, *Camponotus pennsylvanicus* DE GEER, 1773 and *Camponotus chromaiodes* BOLTON, 1995 – increased in abundance in small fragments and in those surrounded by high land-use intensity. The species richness and abundance of myrmecochorous plants were primarily associated with higher abundances of *A. fulva* in large fragments with low land-use intensity, suggesting that seed-dispersing ant species are not functionally redundant in their effects on myrmecochores.

The species composition and abundance of seed-dispersing ants change rapidly across habitat edges, creating boundary dynamics in the interactions between ants and myrmecochorous plants. NESS (2004) found that several seed-dispersing *Aphaenogaster* species declined from forest interiors to edges, which resulted in a net directional movement of seeds of bloodroot (*Sanguinaria canadensis* LINNAEUS) towards the forest interior. *Sanguinaria canadensis* also had shorter seed dispersal distances in forest fragments invaded by *Solenopsis invicta* because they were less effective at dispersing seeds. In a related study, NESS & MORIN (2008) showed that seed predation by rodents was greater along forest edges where ant dispersal of seeds is lower.

The indirect effects of habitat fragmentation on ant-seed mutualisms is reflected in studies that show decreased richness and abundance of myrmecochorous plants in small habitat fragments (GRASHOF-BOKDAM 1997). Likewise myrmecochore richness and abundance are disproportionately lower in linear hedgerows than in forest interiors when compared to plants with other dispersal modes (ROY & DE BLOIS 2006).

Keystone mutualists: In neotropical forests, guilds of ant-following birds feed on swarms of insects that occur during understory raids by army ants, *Eciton burchellii* (WESTWOOD, 1842). Forest habitat area has a strong influence on the number of army ant colonies (PARTRIDGE & al. 1996) and, in turn, the persistence of ant-following bird species in habitat fragments (STOUFFER & BIERREGAARD 1995, STOUFFER & al. 2006). *Eciton burchellii* is particularly sensitive to the loss and isolation of forest habitat because colonies will not move across areas with low canopy cover due to a low tolerance for high surface temperatures (MEISEL 2006). Prey depletion in small forests (< 50 ha) also reduces population size and persistence (PARTRIDGE & al. 1996, BOSWELL & al. 1998). Although several bird species forage opportunistically on insect swarms caused by army ants, obligate ant-following species are particularly sensitive to decreased abundance of army-ant colonies. In a long-term experimental study of forest fragmentation in the tropical rainforest of Amazonas Brazil, STOUFFER & BIERREGAARD (1995) documented local extinctions of three species of obligate ant-following birds within 1 - 3 years following fragmentation into isolated patches 1 - 10 ha in size. Some recolonization of ant-following species occurred 3 - 6 years later as the surrounding matrix became early successional forest, which resulted in increased abundance of army ant colonies. The abundance of ant-following birds in small fragments continued to increase through 10 years later but still had not reached levels recorded in 100 ha patches (STOUFFER & al. 2006). At broader scales, large numbers of bird species are either associated or dependent on army ants in tropical forests. KUMAR & O'DONNELL (2007) observed 41 bird species that were associated with army ant raids along an elevational gradient in Costa Rica. A total of 37 bird species were recorded foraging on insect swarms near ant raids in continuous forests, but only 19 species were found to attend army ant raids in fragmented forests (KUMAR & O'DONNELL 2007).

The functional equivalents of army ants (*Eciton* spp.) in the Old World are the driver ants (*Dorylus* spp.). In African tropical rainforests, 56 species of ant-following birds are associated with driver ants and five species are obligate ant followers (PETERS & al. 2008). *Dorylus wilverthi* EMERY, 1899 and *Dorylus nigricans molestus* (GERSTÄCKER, 1859) are both present in large forest fragments, but *D. wilverthi* occurred less frequently in small fragments. This resulted in lower species richness of ant-following birds in small fragments, particularly specialists, because *D. wilverthi* had a greater daytime activity during the dry season (PETERS & al. 2008). Thus, even the functionally similar *D. nigricans molestus* and *D. wilverthi* show slightly different responses to habitat fragmentation and are not entirely redundant in their effects on bird communities.

Leaf-cutting ants: An interesting contrast to army-ant responses to fragmentation occurs with leaf-cutting ants (*Atta* spp.). *Atta cephalotes* (LINNAEUS, 1758) has a much higher tolerance to surface temperatures than *Eciton burchellii* (reported by MEISEL 2006), and has higher colony densities near forest edge than in the interior (WIRTH & al. 2007). Both *A. cephalotes* and *Atta sexdens* LINNAEUS, 1758 had elevated densities near forest edges, but the density gradient is much steeper for *A. cephalotes* because it prefers to harvest leaves from pioneer tree species near edges whereas *A. sexdens* has a more varied use of substrates for fungus cultures in nests (WIRTH & al. 2007). The greater densities of *Atta* spp. near edges may result in greater leaf-harvesting rates and damage to forest trees (WIRTH & al. 2007), further promoting changes in ecosystem dynamics in small fragments dominated by edge effects (LAURANCE & al. 2002).

Cold climate specialists: In cool temperate forests, ecologically dominant wood ants (*Formica* spp.) vary in response to forest fragmentation depending on the colony structure and habitat suitability. PUNTTILA (1996) examined the colony densities of several *Formica* spp. in boreal forests in Finland. The polygynous *Formica aquilonia* YARROW, 1955 had greater nest densities in the forest interior of older and larger fragments, while colonies of the monogynous *Formica lugubris* ZETTERSTEDT, 1838 were more abundant in small or young forests and near forest edges. The disturbance-tolerant *F. lugubris* and *Formica rufa* LINNAEUS, 1761 have monodomous colonies and defend territories, but eventually are replaced by shade-tolerant *F. aquilonia*, which have polydomous colonies that may occupy large areas through colony budding (PUNTTILA 1996).

MABELIS & CHARDON (2006) studied the metapopulation dynamics of the trunk ant, *Formica truncorum* FABRICIUS, 1804, in isolated patches of open dry woodland in The Netherlands. Within suitable habitat fragments, *F. truncorum* sexuals disperse to form new colonies, which may remain monogynous for long periods of time, or become polygynous and form polydomous colonies by budding and fission (MABELIS & CHARDON 2006). Dispersal between isolated patches only occurs through sexual alates, whereas both dispersal of alates and colony budding occur within patches. The best landscape predictors of habitat occupancy were patch connectivity and perimeter; habitat area was not related to occupancy because colony density was not correlated with patch size. Sexuals were more likely to disperse between adjacent patches with complex habitat boundaries. Extinction rates were greater than colonization, so the metapopulation extinction was predicted within 10 years (MABELIS & CHARDON 2006).

Discussion and conclusions

A recurring theme in studies of habitat fragmentation on ants is the critical importance of boundary dynamics between habitat fragments and the surrounding land use. In my review, virtually all patterns and processes – at the species, functional group, or community level – depend largely on individualistic species responses to changes in the abiotic and biotic gradients along habitat edges. Invasive species, such as *Linepithema humile* or *Solenopsis invicta*, often preferentially colonize edges or disturbances, while edge avoiders, such as *Eciton burchellii* and *Formica aquilonia* are less common in small patches characterized by edge effects. Because ants have key roles in species interactions, differential responses of ant species to habitat boundaries have wide ranging consequences for community and ecosystem dynamics. Clearly we are only beginning to understand how changes in ant species distributions with habitat fragmentation influence species interactions, community composition, and diversity. Although I have emphasized these biotic interactions, large long-lived ant colonies such as wood ants (*Formica* spp.) and seed harvester ants (*Pogonomyrmex* spp.) have important roles in soil nutrient dynamics (MACMAHON & al. 2000, RISCH & al. 2005, WAGNER & JONES 2006), and may be negatively influenced by habitat loss and fragmentation (PUNTTILA 1996, SUAREZ & al. 1998).

Sharp abiotic gradients across habitat edges are central to understanding the mechanisms of ant species responses to habitat fragmentation. The contrasting thermal tolerances of *Eciton burchellii* and *Atta cephalotes* (MEISEL 2006) are specific examples that explain their preferred distributions in forest interior and edges, respectively. More generally, the differential responses of ant genera and subfamilies to habitat disturbances forms the basis of ant functional groups used in ant monitoring for conservation and resource management in human-altered landscapes (BESTELMEYER & WIENS 1996, ANDERSEN & MAJER 2004, MAJER & al. 2007). These patterns extend to regional and continental scales as well, since ant species richness and composition vary strongly in response to changes in climate-energy (temperature, solar radiation) along elevational and latitudinal gradients (KASPARI & al. 2003, DUNN & al. 2007). The variable thermal environments in fragmented landscapes also interact with soil characteristics. Soil disturbance and increased solar radiation in the surrounding land use and along habitat edges change the suitability to ant species that nest in soil or litter. These changes, coupled with natural variation in parent material, often explain significant variation in ant species composition in habitat fragments (DEBUSE & al. 2007, SPIESMAN & CUMMING 2008). The importance of vegetation structure, soils, and the abiotic environment to ants emphasizes the need for a landscape approach that views habitat remnants and surrounding land use as a mosaic of patches which vary in suitability and connectivity to different species (EWERS & DIDHAM 2005, LINDENMAYER & al. 2008).

The sorting of ant species assemblages according to temperature and soil in habitats of different size, connectivity, and surrounding land use helps to explain why ant species richness – a mainstay of conservation biology – often shows little or no relationship to area and isolation. Instead, shifts in species composition occur with habitat fragmentation in which disturbance-tolerant species replace disturbance-sensitive species, often with little or no loss of total species richness. This process of species replacement can be expressed very generally with additive partitions of diversity (CRIST & VEECH 2006). Based on limited data, ant species turnover among habitat fragments occurs at a remarkably constant fraction (0.75) of the overall species richness across a wide range of environments (Fig. 3). Hence, if we have an adequate estimate of the total ant species richness in a landscape or region, we might predict a 75% turnover in species composition across habitats. This aggregate measure does not predict which ant species will be gained or lost among fragments, however, and ultimately individualistic species responses may be important to understanding species interactions and community processes. Nonetheless, a high level of β diversity among habitats is a general property of ant communities, and large turnover in species assemblages among local habitats will affect the outcome of a wide range of species interactions with other insects, plants, and vertebrates.

The effects of turnover in ant species composition on species interactions and ecosystem processes depend on the degree of functional redundancy among ecologically similar ant species (WHITFORD 1997, FOLGARAIT 1998, MACMAHON & al. 2000). For example, does a shift in dominance from *Formica aquilonia* in large, old-growth boreal forest to *Formica lugubris* in small, successional forests documented by PUNTTILA (1996) translate into qualitative changes in species interactions or their effects on soils? Similarly, do changes in the relative abundance of *Aphaenogaster* spp. in large and small fragments of deciduous forest shown by MITCHELL & al. (2002) influence seed dispersal and establishment?

Functional redundancy in community and ecosystem processes is often assessed by defining groups of functionally similar species. In the ant literature, the use of functional groups in monitoring in land management and conservation is based on characteristic responses to ecosystem disturbance, which are consistent across ant subfamilies or genera (ANDERSEN & MAJER 2004). Functional groups defined by responses to disturbance might differ, however, from their functional roles in ecosystems (WHITFORD & al. 1999, SCHOOLEY & al. 2000). For example, North American opportunists may include species of *Formica*, *Myrmica* and *Aphaenogaster*, but the same genera or species may differ considerably in their importance in their roles in interactions with aphids, lycaenids, or myrmecochores (GÓMEZ & ESPADALER 1998, STADLER & DIXON 2005, FIEDLER 2006). The uses of ant functional groups as indicators of ecosystem disturbance and as groups of ants with functionally similar roles in community and ecosystem processes have slightly different objectives, but forging stronger linkages between these approaches would help to increase our understanding of the role of ant biodiversity in ecosystem function. For example, RÍOS-CASANOVA & BESTELMEYER (2008) recently showed that changes in the structure of ant functional groups defined by trophic structure (e.g., granivores vs. scavengers) corresponded to variation in primary production by plant functional groups in different vegetation types.

The roles of species interactions are increasingly recognized in biodiversity conservation. Because ants engage a wide range of facultative and obligate mutualisms, local extinctions of ant species with habitat loss and fragmentation are expected to result in extinctions of mutualistic partners. These "affiliate extinctions" (KOH & al. 2004) may be especially common among ants, and social insects in general (CHAPMAN & BOURKE 2001). The extinction probability of lycaenid butterflies, for example, increases nonlinearly with the extinction risk of the ant host (KOH & al. 2004). Extinction of the army ant, *Eciton burchellii*, a species that is very sensitive to forest patch area, would result in coextinctions of dozens of birds and insects (CHAPMAN & BOURKE 2001, KOH & al. 2004). Some ant species may therefore be considered keystone mutualists and should figure prominently in conservation planning and monitoring.

A poorly known aspect of species responses to habitat loss and fragmentation is the evolutionary change resulting from the altered abiotic environment, shifts in species interactions, or the spread of invasive species (HOFFMEISTER & al. 2005). This is particularly true of ants. A recent study by MÄKI-PETÄYS & al. (2005) showed that rapid genetic change and loss of variation occurred over 30 years in declining populations of the polygynous *Formica aquilonia* with forest fragmentation, but the monogynous *Formica lugubris* was relatively unchanged, suggesting that variation in colony structure has a strong influence on evolutionary responses of ants to fragmentation. In general, ants have several traits – few breeding individuals, social polymorphism, haplodiploidy, and limited queen dispersal – that may lead to low effective genetic population sizes and high extinction risk; conversely, low genetic variation and founder effects might lead to rapid evolution of traits that enable invasive ant species to colonize and spread in disturbed habitats (SEPPÄ 2008). Future work should help elucidate the genetic basis of these vastly different ant species responses to landscape fragmentation.

In conclusion, the central role of ants in understanding the effects of habitat loss and fragmentation is well deserved because of their ubiquity, abundance, diversity and functional roles in ecosystems. Unlike other animal taxa that show clear species-area (DRAKARE & al. 2006) or density-area relationships (CONNOR & al. 2000, HAMBÄCK & al. 2007), however, shifts in species composition with habitat fragmentation are clearly more important for ants than overall richness and diversity. This conclusion is widely supported in the ant literature on ecosystem disturbance and habitat fragmentation (ANDERSEN & MAJER 2004, UNDERWOOD & FISHER 2005, DEBUSE & al. 2007, SPIESMAN & CUMMING 2008). Based on limited data, however, these shifts in composition among fragmented habitats are predictable at the community level, scaling as 75% turnover of the total species pool. With a high degree of turnover in ant species composition in fragmented landscapes, our future understanding of the role of ants in conservation monitoring will hinge on unraveling the ecological and evolutionary responses of ants to landscape change, and determining whether different ant species provide similar functional roles in ecosystems or act as keystone species with no functional equivalents.

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Zusammenfassung

Ameisen sind wegen ihrer Diversität, ihrer Abundanz und ihren funktionellen Rollen in Ökosystemen von zentraler Bedeutung, wenn es darum geht, die Folgen von Verlust und Fragmentierung von Lebensräumen für Gemeinschaften und Ökosysteme zu verstehen. Interaktionen von Ameisen mit anderen Organismen sind weitverbreitet und betreffen andere Insekten, Pflanzen und Wirbeltiere. Ameisen weisen häufig keinen deutlichen Zusammenhang von Artenreichtum und Habitatgröße auf, aber Veränderungen der Artenzusammensetzung von Ameisengemeinschaften folgen einem generellen Muster, mit einem durchschnittlich 75 %igen Turnover der Artenzusammensetzung zwischen Habitatfragmenten. Verschiebungen in der Artenzusammensetzung und relativen Abundanz von Ameisen in Folge von Habitatfragmentierung haben direkte und indirekte Auswirkungen auf Interaktionen mit anderen Organismen, einschließlich die Interaktionen mit Pflanzensaft saugenden Insekten, die Verbreitung von Pflanzensamen und Mutualismen mit Wirbeltieren. In kleinen Habitatfragmenten kann wegen der funktionellen Rollen von Ameisen als Schlüsselarten von Mutualismen sowie bei der Veränderung von Böden bereits der Verlust von einigen Ameisenarten weitreichende Effekte in den Ökosystemen zeitigen. Die von Ameisen ausgehenden dynamischen Effekte zwischen Habitaträndern und der Landnutzung angrenzender Flächen zu durchdringen, ist besonders wichtig für das Verständnis von Habitatfragmentierung, weil steile abiotische und biotische Gradienten das Eindringen invasiver Ameisenarten und drastische Veränderungen der Abundanzen nativer Ameisenarten und der Interaktion von diesen mit anderen Organismen bewirken können.

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