

The Multiple Impacts of Leaf-Cutting Ants and Their Novel Ecological Role in Human-Modified Neotropical Forests

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ABSTRACT

Herbivory has been identified as a potent evolutionary force, but its ecological impacts have been frequently underestimated. Leaf-cutting ants represent one of the most important herbivores of the Neotropics and offer an interesting opportunity to address the role played by herbivorous insects through a perspective that embraces population- to ecosystem-level effects. Here we: (1) qualitatively summarize the multiple ways leaf-cutting ants interact with food plants and their habitats and elucidate the ultimate outcome of such interactions at multiple organization levels; (2) update our understanding of leaf-cutting ant-promoted disturbance regimes; and (3) examine potential ecological roles by leaf-cutting ants within the context of human-modified landscapes to guide future research agendas. First, we find that leaf-cutting ants show that some herbivorous insects are able to generate ecologically important disturbance regimes via non-trophic activities. Second, impacts of leaf-cutting ants can be observed at multiple spatio-temporal scales and levels of biological organization. Third, ecosystem-level effects from leaf-cutting ants are ecosystem engineering capable not only of altering the abundance of other organisms, but also the successional trajectory of vegetation. Finally, effects of leaf-cutting ants are context-dependent, species-specific, and synergistically modulated by anthropogenic interferences. Future research should examine how leaf-cutting ants respond to deforestation and influence remaining vegetation in human-modified landscapes. By promoting either heterogeneity or homogeneity, leaf-cutting ants operate not only as agricultural pests but also as ecological key players.

Abstract in Portuguese is available in the online version of this article.

Key words: *Atta*; ecological filtering; ecosystem engineering; herbivory; human-modified landscapes; microclimatic changes; nutrient cycling; seed dispersal.

HERBIVORES HAVE A VITAL AND MULTI-FACETED ROLE IN MODULATING SPECIES and trait evolution (Agrawal 2011), structuring plant communities (Huntly 1991, Maron & Crone 2006, Allan & Crawley 2011), and shaping ecosystem functioning (Belovsky & Slade 2000, Weisser & Siemann 2004). How herbivory by insects affects plant population and community ecology and ecosystem processes remains poorly studied, however, despite calls for more research into this issue (Weisser & Siemann 2004). Such demand is now fueled by the fact that the interactions between plants and herbivores are likely to experience changes induced by global-scale anthropogenic disturbances (Tscharrntke *et al.* 2002, Valladares *et al.* 2012).

One potential scenario is that many human-modified landscapes will experience a boom in herbivory (Coley 1980, 1998, Tylianakis *et al.* 2008, Wirth *et al.* 2008). The ubiquitous spread of fast-growing plant species (Tabarelli *et al.* 2012a), which tend to be poorly defended against herbivores (Coley *et al.* 1985), might play a crucial role as causal mechanism here—the spread of these species is promoted by disturbance-driven resource release in the wake of habitat fragmentation (Laurance *et al.* 2006, Santos *et al.* 2008) and anthropogenic nitrogen deposition (Dukes

& Mooney 1999). In addition, herbivores may capitalize on the predicted rise in temperature (Bale *et al.* 2002) or increase their consumption rates in elevated CO₂ environments to compensate for the expected decline in leaf nutritive quality (Ayres 1993). In fact, human-disturbances are rapidly converting intact tropical landscapes into human-modified ones (Melo *et al.* 2013), with impacts on herbivore abundance and species richness (Arnold & Asquith 2002, Wirth *et al.* 2008). There is now ample evidence that while numerous habitat and dietary specialists decline or remain at low abundance in human-altered habitats, a small set of species thrive following disturbance (Didham *et al.* 1998, Tscharrntke *et al.* 2002, Tabarelli *et al.* 2010). However, our understanding of impacts of these species across multiple ecological levels (*i.e.*, from organism to ecosystem functioning) remains limited.

The leaf-cutting ants (LCA) *sensu stricto* (genera *Atta* and *Acromyrmex*, Myrmicinae) are an ideal system for understanding the impacts of species that proliferate in human-modified landscapes (Wirth *et al.* 2007, Tabarelli *et al.* 2012a). There are currently 40 recognized species of LCA (Schultz & Brady 2008). They share a distinct set of morphological, metabolic, and natural history characters, together with the unique habit of cutting fresh leaf material to cultivate a symbiotic fungus that serves as their main food source (Weber 1966, Mueller *et al.* 1998, De Fine

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Licht & Boomsma 2010, Hölldobler & Wilson 2011). This ecological group is present in the majority of Neotropical and subtropical habitats, from native forests to pasturelands and agricultural fields (Weber 1966, Farji-Brener & Ruggiero 1994). Some species have narrow geographic distributions or are habitat specialists (e.g., *Atta robusta*, Teixeira *et al.* 2003), while others are generalist and widely distributed (e.g., *Atta sexdens*, Fowler *et al.* 1989). In addition, they are major agricultural pests (for review see Montoya-Lerma *et al.* 2012). They harvest tremendous quantities of plant biomass (Wirth *et al.* 2003, Herz *et al.* 2007, Costa *et al.* 2008), act as ecosystem engineers in part due to the size and longevity of their nests (Corrêa *et al.* 2010, Meyer *et al.* 2011a,b, 2013), and have long-been the subject of studies of herbivory (e.g., Herz *et al.* 2007) that can provide baseline data against which to compare the impacts of their outbreaks in disturbed habitats (Urbas *et al.* 2007).

In this review we: (1) synthesize the multiple ways LCA interact with food plants and their habitats and elucidate the ultimate outcome of such interactions at multiple organization levels, by paying particular attention to context dependency or conditions that promote it; (2) update our comprehension about LCA-promoted disturbance regimes and place this in the current perspective about the role played by insect herbivores; and (3) examine potential ecological roles played by LCA in human-modified landscapes to guide future research agendas. To do so, we reviewed over 160 articles covering seven decades of research. This sample represents the vast majority of the articles indexed in the Web of Science, using 'leaf-cutting ants' and 'plants' as search strings. Available literature is clearly biased in terms of duration, ecosystem, LCA species, ecological processes, and research groups. With these limitations in mind, we aim to summarize the available information and present LCA-mediated effects as plausible and ecologically relevant working hypotheses, rather than definite conclusions for how leaf-cutting ants affect biological organization from population to ecosystem levels.

The article is divided into three major sections. In sections one and two, we examine the trophic impacts of LCA via herbivory and seed harvesting, then analyze the consequences of (non-trophic) engineering activities. Throughout these topics, we pay particular attention to the forces modulating ant activity and the potential plurality of impacts across multiple spatial scales and levels of biological organization: from individual plants to population (plant fitness, demography), community, and ecosystem levels (patterns of nutrient cycling), as well from small (ant nest area) to larger spatial scales (foraging areas). Finally, we address a potential shift or expansion of the ecological role of LCA as human populations continue to alter Neotropical landscapes and propose a research agenda based on our conclusions.

LCA AND THEIR FOOD PLANTS: CONTEXT-DEPENDENT IMPACTS VIA HERBIVORY AND SEED HARVESTING

One of the most striking features of LCA is, undoubtedly, their role as generalist herbivores. Depending on colony size and spe-

cies, rates of plant consumption per colony ranging from *ca* 70 to 500 kg (dry weight) annually for the cultivation of their symbiotic fungus turns *Atta* ants into the preeminent herbivore of Neotropical forests and savannas (Wirth *et al.* 2003, Herz *et al.* 2007, Costa *et al.* 2008 and references therein). Leaf-cutting ants achieve such high rates of biomass consumption through complex and highly organized foraging/transportation devices, usually in the form of thoroughly cleared, up to 30 cm wide trunk trails, sometimes extending more than 250 m from the nest into the foraging territories (Hölldobler & Wilson 2011), which cover areas often as large as one to two hectares (Wirth *et al.* 2003, Urbas *et al.* 2007, Silva *et al.* 2009). These foraging systems appear to be extremely flexible, allowing LCA to profit from the continuous emergence/recruitment of palatable resources (Silva *et al.* 2013). Assuming a density of up to five adult colonies per hectare (Wirth *et al.* 2007), some habitats (e.g., early successional forests) can be entirely exposed to LCA foraging activity (Silva *et al.* 2009), although harvesting is closely confined to plants directly accessible via the foraging trail network (Kost *et al.* 2005).

Leaf-cutting ants can be considered generalist herbivores with a high degree of polyphagy, consuming up to 50 percent of the local forest flora (Vasconcelos & Fowler 1990, Wirth *et al.* 2003) and ingesting a rich diversity of plant matter (e.g., leaves, twigs, bark, flowers, fruits, seed endosperm [Wirth *et al.* 2003, Falcão *et al.* 2011]). Despite this dietary opportunism, LCA show a remarkable selectivity within the available spectrum. There is a preference for: (1) long-lived resources, such as leaves from large trees (Cherrett 1968, Blanton & Ewel 1985, Wirth *et al.* 2003, Falcão *et al.* 2011); (2) young leaves (Rockwood 1976, Nichols-Orians & Schultz 1990, Mundim *et al.* 2008), although, if flowers and fruits are available, they tend to collect these more energetic plant parts (Wirth *et al.* 2003, Falcão *et al.* 2011); (3) drought-stressed individuals or leaves with increased nutrient contents (Blanton & Ewel 1985, Vasconcelos & Cherrett 1996, Meyer *et al.* 2006, Mundim *et al.* 2008, Ribeiro Neto *et al.* 2012); (4) individuals lacking induced defenses (Kost *et al.* 2011); (5) pioneer species with fewer chemical defenses (Farji-Brener 2001, Wirth *et al.* 2003, Falcão *et al.* 2011); (6) species with less physical defenses (Howard 1988, Nichols-Orians & Schultz 1989); (7) plant species with which workers have no previous experience (Saverschek *et al.* 2010) such as exotic species (Blanton & Ewel 1985); and (8) leaves with low loads of foliar endophytic fungi (Bittleston *et al.* 2011, Estrada *et al.* 2013). In synthesis, the selection of suitable food plants by LCA is a complex, multivariate decision-making process involving the assessment of multiple plant traits, environmentally induced factors, and the individual foraging history of the ants.

On the individual plant level, LCA can remove up to 40 percent of the annual leaf area production. However, removal rates ranging from less than 10 to *ca* 30 percent are probably more common, especially for highly preferred tree and liana species (Wirth *et al.* 2003). At the community level (or at the spatial scale of their foraging area), LCA have been shown to remove 8–15 percent of the available leaf area of Neotropical forests (Wirth *et al.* 2003, Urbas *et al.* 2007) and 13–17 percent of the Cerrado

savanna (Costa *et al.* 2008). Recent work has revealed remarkable context dependency of LCA herbivory pressure across forested ecosystems, with it being strongly linked to the proportion of pioneer plant species present in a site (Rao *et al.* 2001, Urbas *et al.* 2007, Wirth *et al.* 2008, Falcão *et al.* 2011). In fragmented landscapes, particularly along forest edges and in regenerating secondary forests where pioneer species predominate (Laurance *et al.* 2006, Santos *et al.* 2008), LCA exhibit smaller foraging areas (Urbas *et al.* 2007, Silva *et al.* 2009) and increased colony density (Wirth *et al.* 2007, Meyer *et al.* 2009, Silva *et al.* 2009, Dohm *et al.* 2011, Carvalho *et al.* 2012). Together with the fact that these colonies harvest equal amounts of biomass, smaller foraging areas (*e.g.*, 0.9 vs. 2.3 ha/col/yr, Urbas *et al.* 2007) result in higher herbivory rates per colony.

Such rates of damage are likely to affect the individual performance and the fitness of plant populations, given that an annual leaf loss of 10 percent is considered sufficient to reduce the reproductive success of many tropical tree species (Dirzo 1984, Marquis 1984). Herbivory by *Atta cephalotes* and *A. sexdens* in the Atlantic forest, for example, reduced the production of flower and/or fruits in *Lacistema robustum* (Lacistemaceae), *Leandra rufescens*, *Miconia nervosa* (Melastomataceae), *Psychotria deflexa*, *P. platypoda* and *P. racemosa* (Rubiaceae), and *Vismia guianensis* (Clusiaceae) relative to that of plants that had been protected from LCA harvest for 2 yr (Leal *et al.* 2012). Though it is known

that the effect of herbivory on plant reproduction is strongly influenced by life history strategies (*e.g.*, Koptur *et al.* 1996), plant tolerance to herbivory (Fornoni 2011), and factors such as the timing of herbivory relative to the developmental stage (Marquis *et al.* 1997), the reproductive losses inflicted by LCA are likely driven by the loss and/or reallocation of photosynthetic resources (*e.g.*, for compensatory responses; Trumble *et al.* 1993). This interpretation has recently gained support from clipping experiments by Mundim *et al.* (2012) indicating plant species are not tolerant to simulated herbivory by *Atta*, resulting in reduced flowering, plant architecture, and survivorship.

In synthesis, the impact of LCA herbivory on plants is mostly negative and may be modulated by multiple ecological factors at different spatial scales (Fig 1). On the individual plant level, effects are probably more intense during the plant's reproductive stages, as flowers, fruits, and seeds are preferred food items that are energetically expensive to produce and are directly related to plant fitness. Similarly, young plants or plants bearing young leaves are expected to suffer from high LCA herbivory. In addition, the susceptibility to LCA likely increases for plant individuals under drought stress, which osmoregulate via the accumulation of amino acids and carbohydrates, and thus are more nutritious to the ants. On the population level, LCA impacts may be stronger in the case of small populations or those populations around nests and foraging trails, where ants concentrate their

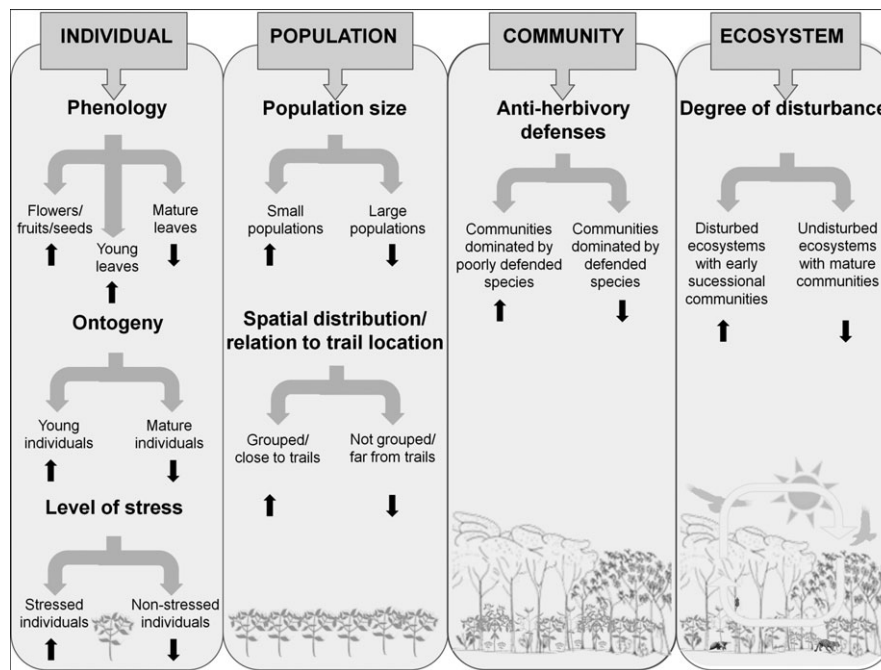


FIGURE 1. Potential factors modulating leaf-cutting ant herbivory and its potential effects from individual plants to the ecosystem level (modified from Leal *et al.* 2012). Inequality signs indicate high (↑) vs. low (↓) relative impact of leaf-cutting ant herbivory. At the individual level, plants at reproductive stages, young individuals or individuals bearing young leaves, and stressed individuals are more vulnerable to experience intense herbivory by leaf-cutting ants with more pronounced effects in terms of fitness. At the population level, small plant populations with clustered individuals located around foraging nests and trails are more vulnerable and may experience increased rates of herbivory. Plant communities dominated by undefended species and those species in disturbed ecosystems are more vulnerable to intense herbivory.

cutting activities. At the community level, plant communities dominated by less resistant species appear to suffer greater biomass loss to herbivores. Finally, LCA abundance increases in disturbed ecosystems, resulting in higher damage to the vegetation and supporting the notion that their importance as herbivores is more prominent in disturbed habitats (Fig. 1).

Leaf-cutting ants collect substantial amounts of seeds and fruits to grow their fungus gardens and, thus, act as seed dispersers and predators (Silva *et al.* 2009 Ferreira *et al.* 2011). Such fruit/seed collections can be immense, for example up to 160,000 *Miconia* fruits per day (Wirth *et al.* 2003). In the Atlantic forest, local *Atta* species preferentially collect berries and drupes bearing small-sized seeds (≤ 15 mm length), such as those from Melastomataceae, Anacardiaceae, and Solanaceae (Costa *et al.* 2014). These plant taxa represent an important component of the pioneer flora in this biota (Grillo *et al.* 2006), indicating that pioneer species may benefit by interacting with LCA (Costa *et al.* 2014).

Seed manipulation by LCA includes carrying them to the subterranean nests and deposition on refuse dumps outside the nest, often after the fleshy fruit or arils have been removed or exhausted by the symbiotic fungus (Farji-Brener & Silva 1996, Wirth *et al.* 2003). Some LCA species also leave seeds in subterranean refuse chambers or fungus gardens, where they die (Moutinho *et al.* 1993, Farji-Brener & Medina 2000). Finally, seeds may be lost along ant trails during transport to the nest (Dalling & Wirth 1998, Leal & Oliveira 1998).

The removal of fruit pulp, seed movement, and seed deposition in different microenvironments can have both positive and negative implications for the germination and recruitment of seedlings and ultimately plant demography. There are reports of reduced intra- (Byrne & Levey 1993) and interspecific (Loiselle 1990) competition among seedlings originating from seeds defecated by vertebrates and subsequently dispersed by ants on savanna and forest floors (*e.g.*, Leal & Oliveira 1998, Passos & Oliveira 2003, Pizo *et al.* 2005). Seed cleaning can also enhance germination by reducing fungal pathogen attack on fallen fruits (Oliveira *et al.* 1995, Farji-Brener & Silva 1996, Leal & Oliveira 1998), as can deposition of seeds on ant nests (Leal & Oliveira 1998, Silva *et al.* 2007). These nests may be nutrient-rich (*e.g.*, Farji-Brener & Ghermandi 2000, 2008, Farji-Brener & Medina 2000, Moutinho *et al.* 2003, Pinto-Tomás *et al.* 2009) or have temperature or moisture regimes that enhance germination (Horvitz 1981).

The potential effects of seed dispersal by LCA on plant recruitment and establishment are still poorly understood, as in the majority of studies, seed fate has been monitored through germination. Two studies in the Atlantic forest have documented elevated mortality following the defoliation of seedlings that germinated from seeds aggregated by LCA around their nests (Silva *et al.* 2007, Corrêa *et al.* 2010). Additionally, repeated defoliation events appear to be the primary cause for reduced seedling survival of six Atlantic forest tree species on *A. cephalotes* nests (Meyer *et al.* 2011b). On the other hand, higher plant recruitment has been observed on *Atta laevigata* and *Acromyrmex lobicornis* nests

in ecosystems with shallow, rocky, and nutrient-poor soils, such as Venezuelan savannas and Patagonian grasslands (*e.g.*, Farji-Brener & Silva 1995a,b, 1996, Farji-Brener & Ghermandi 2000, 2008). Regardless of whether the effects of LCA on seed recruitment are positive or negative, their effects on plant populations could be potent forces driving community-level changes at spatial scales far beyond ant nests. Seedling and sapling assemblages differed markedly around nest and foraging areas when compared to control sites unaffected by the colonies; community composition also ultimately converged around nests when compared to control sites (Corrêa *et al.* 2010, Meyer *et al.* 2011b, Silva *et al.* 2012). These findings indicate that ant-induced disturbance regimes may act as ecological filters (*sensu* Belyea 2004) for plant establishment (Meyer *et al.* 2011b, Silva *et al.* 2012).

In summary, variation in the outcome of LCA-seed dispersal interactions can be attributed to at least four factors: (1) ant behavior toward diaspores, (2) the final seed deposition site, (3) defoliation suffered by seedlings establishing on ant nests, and (4) the soil quality for plants (Fig. 2). Seed cleaning without seed removal from the parental neighborhood is expected to impose a negative effect on recruitment, as seeds and resulting seedlings will remain/concentrate beneath parental trees (pathway 1). By cleaning seeds from vertebrate feces, which are already less aggregated and far from parental plants, ants may reduce fungal seed infections and enhance recruitment (pathway 2). Seed removal and loss along foraging trails reduces seed aggregation and enhances the probability of seed deposition in microsites suitable for germination (pathway 3). Among the seeds carried toward ant nests, those discarded inside nests do not germinate (pathway 4), whereas those deposited in external refuse dumps allow the recruitment of new plants. For seeds germinating on the nest surface, successful plant recruitment depends on the intensity of defoliation. Intense damage prevents seedling establishment (pathway 5), however, moderate damage may be tolerated by seedlings in cases where nest soil has elevated nutrients relative to nearby nutrient-limited soils (pathway 6). On the other hand, if the nests are environmentally similar to adjacent areas, seed deposition on ant nests is likely to offer little or no advantage for plant recruitment (pathway 7).

ECOSYSTEM ENGINEERING VIA NEST KEEPING AND FORAGING

Many organisms are able to modulate the spatio-temporal availability of resources by directly or indirectly altering their physical environment. In doing so, these so-called ecosystem engineers (Jones *et al.* 1994) modify, maintain, and create habitats for other species. It has become apparent that the ecological role of LCA goes far beyond direct trophic effects of herbivory and seed dispersal to include the transformation of habitats. The impact of LCA as soil ecosystem engineers is primarily a consequence of nest construction and maintenance. The colossal nests of the genus *Atta* are composed of up to 8000 subterranean interconnected chambers reaching as deep as 7–8 m underground (Moreira *et al.* 2004a,b), an extensive system of foraging and

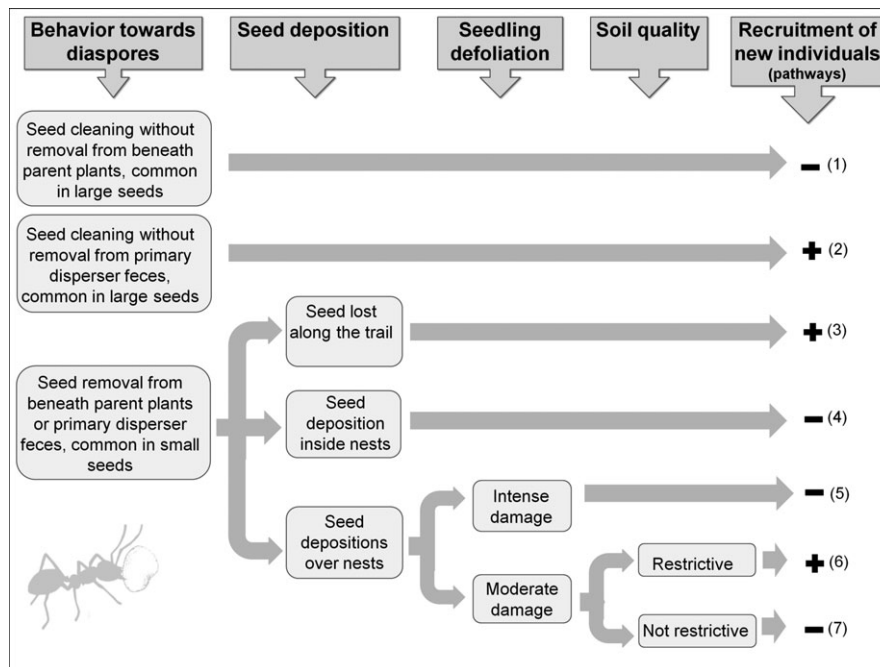


FIGURE 2. Potential factors modulating the impact of seed dispersal by leaf-cutting ants on plant recruitment (modified from Leal *et al.* 2012). Seed cleaning without seed removal from near parental plants is expected to impose a negative effect on recruitment because seeds and resulting seedlings will persist in aggregations beneath parents (pathway 1). By cleaning seeds from vertebrate feces, ants reduce fungal attack on seeds resulting in a positive effect (pathway 2). Seed removal and loss along foraging trails reduces seed aggregation and enhances the probability of seed deposition in a habitat suitable for germination (pathway 3). Seeds discarded inside nests do not germinate (pathway 4), while those deposited outside nests are able recruit as new plants. For seeds germinating on nest surfaces, successful plant recruitment is influenced by herbivory on seedlings. Intense damage prevents seedling establishment (pathway 5), while moderate damage levels may be tolerated by seedlings in cases where nest soils are more suitable sites for plant recruitment than adjacent areas (pathway 6). Conversely, if the nests are environmentally similar to adjacent areas, seed deposition on ant nests is likely to offer little or no advantage for plant recruitment (pathway 7).

ventilation tunnels, and large mounds of soil above their surface reaching up to 250 m² in area (Cherrett 1989). For the construction and maintenance of these structures, LCA move large quantities of soil—sometimes more than 20 m³ or 40 tons—to the surface (see Farji-Brener & Illes 2000 and Hölldobler & Wilson 2011 for a revision). The ants constantly maintain the chambers, tunnels, nest entrances, and nest mounds, and also transport soil materials, exhausted fungus, and other organic detritus into subterranean waste chambers or on the nest surface (Farji-Brener & Illes 2000, Wirth *et al.* 2003, Herz *et al.* 2007). In addition, the majority of *Atta* species maintain an open area free of plants and debris (nest clearings) by routinely clearing and defoliating above their nests (Farji-Brener & Illes 2000, Corrêa *et al.* 2010, Meyer *et al.* 2011a,b).

Nest construction and maintenance, therefore, alter the physical and structural nature of soils and the spatial distribution of nutrients during and after the life of a colony (Garrettson *et al.* 1998, Sousa-Souto *et al.* 2008, Hudson *et al.* 2009, Bieber *et al.* 2011), especially through deposition of materials/nutrients at nest scale (*e.g.*, Haines 1978, Garrettson *et al.* 1998, Moutinho *et al.* 2003). Extensive networks of galleries and chambers augment soil porosity, aeration, water infiltration, and drainage (Cherrett 1989). In addition, the continued deposition of mineral soils to the nest surface by ant workers (*i.e.*, the inversion of soil layers) can

produce a new edaphic horizon—a new horizon A1 (Alvarado *et al.* 1981, Meyer *et al.* 2013). Because the organic residuals of the colony remain in the nest interior (waste chambers) in most *Atta* species (Farji-Brener & Illes 2000, Sousa-Souto *et al.* 2008, Bieber *et al.* 2011), this new horizon generally has elevated mineral content and poor nutrients. The soils of nest mounds also contain reduced organic material (Meyer *et al.* 2013) due to nest clearing operations removing vegetation and leaf litter from the immediate nest surface (Meyer *et al.* 2011a, 2013).

On the other hand, portions of nest mounds that receive the organic detritus of the colonies (*i.e.*, external waste deposition) may contain increased concentrations of nitrogen and phosphorus (Farji-Brener & Silva 1995b, Farji-Brener & Medina 2000). In fact, the presence of sites with enriched topsoils ('islands of fertility') has been described as an engineering activity of LCA. It alters resource availability and favors plant recruitment (Farji-Brener & Ghermandi 2000, Sosa & Brazeiro 2010, 2012), including that of exotic plant species (Farji-Brener & Ghermandi 2008, Farji-Brener *et al.* 2010). This can influence the maintenance of biological diversity, given that these sites allow for niche partitioning among plant species (Garrettson *et al.* 1998, Farji-Brener & Illes 2000, Farji-Brener 2005, Hudson *et al.* 2009). In some non-forested ecosystems (*e.g.*, Venezuelan savannas and Patagonian grasslands), LCA nests function as nurse elements by creating

safe sites for the colonization and establishment of tree and shrub species. This can result in islands of arboreal vegetation in a matrix dominated by steppe or savanna and soils that are otherwise unfavorable for recruitment (Jonkman 1978, Farji-Brener & Silva 1995a,b, 1996, Farji-Brener & Ghermandi 2000, 2008, Sousa-Souto *et al.* 2007, Farji-Brener *et al.* 2010, Sosa & Brazeiro 2010, 2012). Interestingly, individuals growing in those richer soils develop better physical defenses against herbivory, such as larger and denser spines (Farji-Brener 2007).

In forested ecosystems, however, the effects of ant nests on regenerating plants may be negative when refuse chambers are internal and ants reduce the litter cover (bare-soiled nest clearings) and hence depress nutrient availability (Meyer *et al.* 2013). Recruited seedlings may be buried or experience defoliation while leaf litter is removed during nest cleaning (Meyer *et al.* 2011a,b, 2013). Furthermore, external refuse piles have a lower diversity of seed species (Farji-Brener & Medina 2000), than areas unaffected by LCA. In contrast, a greater abundance of fine roots has been documented in the nest topsoil of external refuse dumpers such as *A. colombica* (Farji-Brener & Medina 2000), suggesting that neighboring plants can access these nutrients via root growth. This suggests that the location of LCA refuse dumps can have positive or negative effects on plant regeneration that remain to be systematically examined.

Apart from the shifts in topsoil layers while colonies are active, LCA nest environments also experience modifications of the AB and B horizon through (1) the accumulation of organic material in the waste chambers and fixation of atmospheric N₂ via symbiotic associations with nitrogen-fixing bacteria in the fungus gardens (Verchot *et al.* 2003, Pinto-Tomás *et al.* 2009); (2) removal of mineral materials, such as clay and sand; and (3) diffusion or leaching of nutrients (Alvarado *et al.* 1981, Moutinho *et al.* 2003, Wirth *et al.* 2003). Deep soils (>1 m), especially in species with underground waste chambers, contain higher concentrations of cations, inorganic nitrogen, and organic matter than non-nest soil (Farji-Brener & Medina 2000, Moutinho *et al.* 2003, Verchot *et al.* 2003, Sousa-Souto *et al.* 2008). Nutrient cycling is likely to be incomplete because considerable portions of these deep nutrient patches are inaccessible for plant roots (shallow-rooted seedlings or species) and tend to be leached into lower horizons (Verchot *et al.* 2003). However, adult trees may benefit from LCA deep soil enrichment—coarse and fine roots can be more abundant in nest-associated subsoils (Moutinho *et al.* 2003, Verchot *et al.* 2003, Sousa-Souto *et al.* 2008). Not only plants are influenced by LCA activities. There can also be an increased abundance of soil micro-organisms and litter arthropods in the waste piles of external refuse dumpers (Rojas 1989, Moser 2006, Farji-Brener 2010); their presence could feedback on plant recruitment, growth, and other trophic interactions (Wirth *et al.* 2003, Farji-Brener *et al.* 2009). Similarly, a wealth of interactions can be expected to emerge from recent reports of a highly diverse microbial community associated with LCA fungal gardens (Pinto-Tomás *et al.* 2009, Schoenian *et al.* 2011).

When LCA colonies with internal refuse dumps die or migrate, nest topsoils tend to remain nutrient-poor compared to

adjacent forest areas for a long time (Bieber *et al.* 2011, for *Atta cephalotes*). In addition, nest soils can become compacted and impenetrable due to continued exposure to radiation and rainfall, reducing plant recruitment up to 15 yr after nest abandonment (Bieber *et al.* 2011). Even in the case of external refuse, the ‘island of fertility’ is a transient phenomenon. Nutrient concentrations decline rapidly in nest sites abandoned for more than 1 yr (Hudson *et al.* 2009, for *Atta colombica*) probably due to leaching. All these results reinforce the notion that nest building and maintenance activities are changing soil properties and acting as potential ecological filters (*sensu* Belyea 2004) for seedling establishment (Bieber *et al.* 2011, Meyer *et al.* 2011b, 2013, Leal *et al.* 2012), while adult trees may benefit.

Briefly, LCA effects on plant recruitment via changes in soil attributes are apparently conditioned by four key factors: (1) the location of the refuse dump; (2) the occurrence of leaf litter removal; (3) the environmental soil quality in the nest vicinity; and (4) the relative importance of niche partitioning as a mechanism promoting plant species coexistence (Fig. 3). External waste deposition may turn LCA nests into important recruitment sites, especially when litter is not removed. Positive effects can be enhanced when soil around nest sites is of poorer quality and in the presence of niche partitioning as effective mechanism of plant species coexistence (pathway 1). Other combinations of soil quality and niche partitioning may have negligible or even neutral effects in terms of plant recruitment and plant species diversity as a consequence of changes in soil or nutrient dynamics mediated by nest presence (pathways 2–3). In the case of moderate litter removal but with good-quality soils around nests and the lack of intense plant competition, nest sites may be less suitable habitats for recruitment than nearby forest (pathway 4); the same may be true with intense leaf litter removal (pathway 5). In the case of belowground waste disposal (most *Atta* species), LCA are expected to enhance plant recruitment and species coexistence, especially in poor soils (pathway 6). However, the positive effect must be less intense than for those species with external refuse dumps (pathway 1). Again, particular combinations of soil quality and niche partitioning may have neutral effects on recruitment (pathways 7 and 8). In other situations, ants may create environments with physical barriers for recruitment (*e.g.*, compacted mineral soils with little penetrability), retarding regeneration after colonies die (pathway 9 and, in the most negative case, pathway 10). As the colony dies or the nest is abandoned, some soil attributes altered by LCA may change rapidly (*e.g.*, increased concentrations of nitrogen and phosphorus, Hudson *et al.* 2009) or manifest themselves after several years (*e.g.*, reduced carbon content and organic matter, Bieber *et al.* 2011). Other drastic changes can persist for decades after nest abandonment (*e.g.*, soil compaction, Bieber *et al.* 2011).

Physical engineering by LCA can also include modifications of light regimes by altering the vegetation in understory and canopies. In the case of Neotropical forests, ants of the genus *Atta* have been shown to alter the light availability at the nest surface (Farji-Brener & Illes 2000, Hull-Sanders & Howard 2003, Corrêa *et al.* 2010, Meyer *et al.* 2011a) and in the foraging area (Wirth

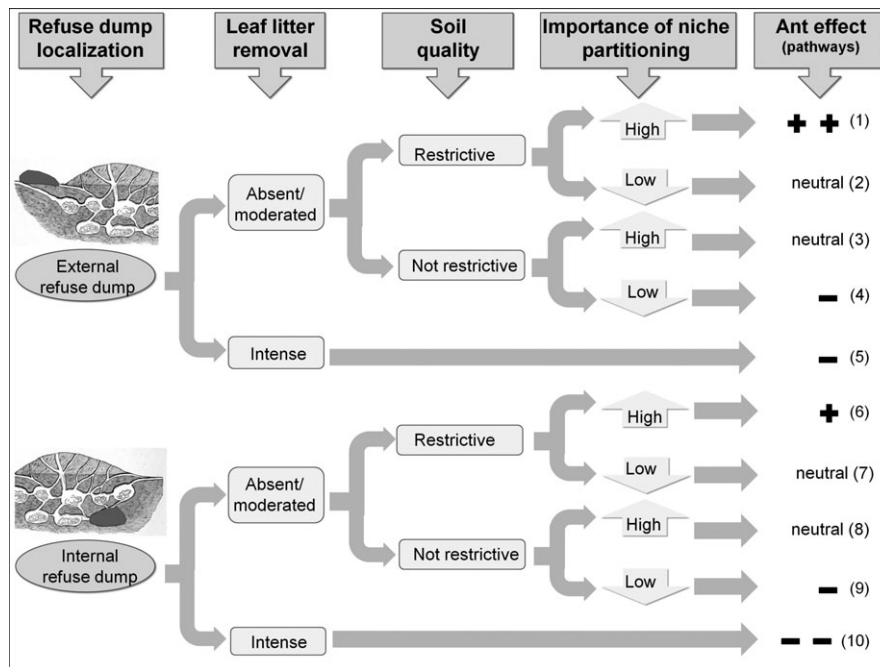


FIGURE 3. Factors modulating potential impacts of LCA on plant recruitment via changes in soil attributes (modified from Leal *et al.* 2012). External waste deposition may turn leaf-cutting ant nests into important recruitment sites, especially when (1) litter is not removed, (2) when soil around nest sites is not suitable for recruitment and (3) when there is niche partitioning by plant species promoting coexistence (pathway 1). In the case of moderate leaf litter removal but with good-quality soils around nests and minimal plant competition, nest sites may represent less suitable habitats for recruitment (pathway 4); the same may be true when there is intense leaf litter removal (pathway 5). In the case of belowground waste disposal, leaf-cutting ants are expected to positively affect plant recruitment and species coexistence, especially in the context of poor soils and niche partitioning (pathway 6); this positive effect will be less intense than for those species with external refuse dumps (pathway 1). Other combinations of soil quality and niche partitioning may result in neutral effects on recruitment (pathways 2, 3, 7 and 8). Finally, ants may impose physical barriers for plant recruitment (*e.g.*, compacted mineral soils with little penetrability), retarding plant recruitment and regeneration after colonies die (pathways 9 and 10, the latter being the worst case). As the colony dies or the nest is abandoned, some of the soil attributes altered by LCA may disappear rapidly (*e.g.*, increased concentrations of nitrogen and phosphorus, Hudson *et al.* 2009) or persist for several years after nest inactivity (*e.g.*, reduced carbon content and organic matter, Bieber *et al.* 2011). Other attributes experience drastic shifts for decades after nests become inactive (*e.g.*, soil compaction Bieber *et al.* 2011).

et al. 2003, Leal *et al.* 2012). The constant removal of vegetation growing on or overhanging the nest surface results in two types of clearings—those in the understory ('bottom-up' gaps, *sensu* Farji-Brener & Illes 2000) and those in the canopy (Corrêa *et al.* 2010, Meyer *et al.* 2011a). Both of these can be maintained during the lifetime of a colony. Studies of *A. cephalotes* in the Atlantic forest revealed that canopy openness above colonies increased by roughly 50 percent, allowing three times as much light to reach the forest floor compared to non-nest sites. This also increased daily temperature amplitudes and reduced soil moisture content on the nest mounds (Corrêa *et al.* 2010, Meyer *et al.* 2011a). Changes in light level were not restricted to the nest site itself, but extended up to about 4 m beyond the nest edge into the surrounding forest (Meyer *et al.* 2011a). As the colony dies or the nest is abandoned, light levels may rapidly return to those similar to areas not affected by LCA (see Bieber *et al.* 2011).

The increased availability of light, regardless of whether it arises from the clearing of vegetation above nests or from foraging activities in the canopy, can affect the recruitment and structure of plant assemblages, and is thus another means by which

LCA can engineer ecosystems (Garrettson *et al.* 1998, Hull-Sanders & Howard 2003, Wirth *et al.* 2003, Corrêa *et al.* 2010, Meyer *et al.* 2011a,b, Leal *et al.* 2012). Nevertheless, despite the positive impacts of increased light on some plants, nest clearing also involves lethal defoliation of many plants on the nest surface (Meyer *et al.* 2011a). Thus, active colonies with nest clearings may also support seedling assemblages with fewer plants and lower species richness (Corrêa *et al.* 2010, Meyer *et al.* 2011b). Again, there is evidence that LCA impose ecological filters for plant establishment as part of their ecosystem engineering activities (Corrêa *et al.* 2010, Meyer *et al.* 2011a,b, Leal *et al.* 2012).

Hypotheses and empirical evidence regarding the engineering impacts of LCA suggest that their potential effects on plant recruitment and species coexistence may be modulated by three factors: (1) the type of forest gap resulting they create (*i.e.*, canopy vs. understory gaps); (2) the intensity and extent of increased light; and (3) the relative importance of niche-based mechanisms for plant coexistence. As synthesized in Figure 4, three groups of possibilities emerge. Nest clearings occurring in vegetation types with reduced light availability but high competition for light are

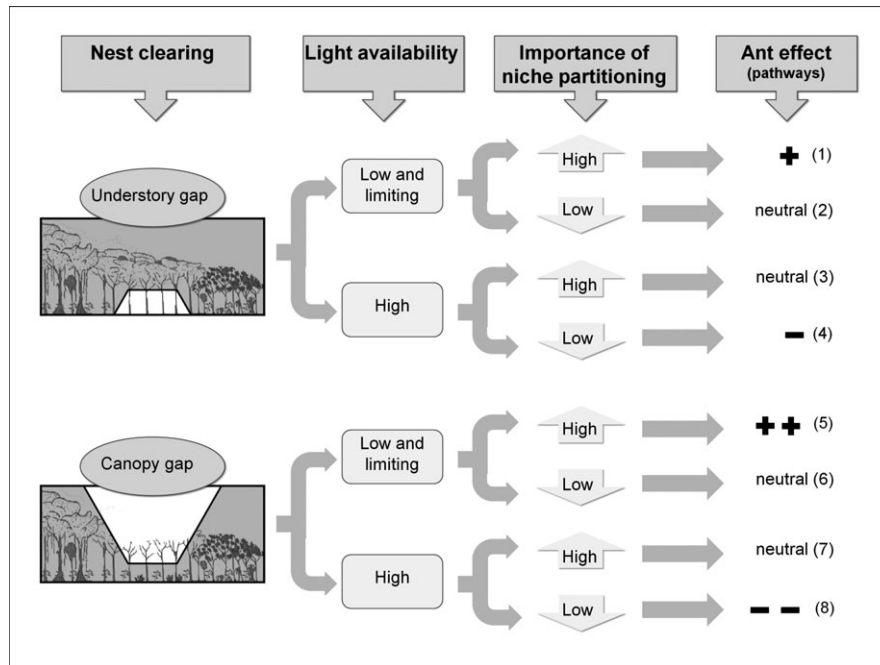


FIGURE 4. Factors modulating potential impacts of LCA on plant recruitment via shifts in light regimes (modified from Leal *et al.* 2012). In vegetation types with reduced light availability but high plant competition for light, canopy gaps are expected to generate far more positive effects for plants and their assemblages (pathway 5) than understory gaps (pathway 1). Conversely, in those situation marked by elevated light availability, ants are expected to play a negative role (pathway 4 and 8). Where light is limiting but niche partitioning is irrelevant (pathways 2 and 6) or light is not limiting but niche partitioning plays an important role (pathways 3 and 7), the effect of leaf-cutting ants may be neutral. The single paper measuring light regime in LCA-inactive nests shows that after 5 yr of colony death or nest abandonment light regime is similar to those areas not affected by LCA (Bieber *et al.* 2011).

expected to have positive effects, with light-rich canopy gaps (pathway 5) more beneficial than understory ones (pathway 1). In contrast, in already illuminated habitats such as forest edges, ant-created increases in canopy openness could reduce recruitment of desiccation-sensitive plant species (pathways 4 and 8). The effect of LCA may be neutral where light is limiting but niche partitioning is irrelevant (pathways 2 and 6) or light is not limiting but niche partitioning plays an important role (pathways 3 and 7). Considering the longevity of *Atta* colonies (*e.g.*, 7–10 yr, Weber 1972, Meyer *et al.* 2009), the impact of their canopy openings is less transient than that of tree fall gaps, in which canopy cover can return to pre-gap levels within 2 yr (Fraver *et al.* 1996).

We draw five conclusions regarding LCA ecology and their disturbance regimes. First, LCA can have ecologically relevant impacts via non-trophic activities. Second, the impacts of LCA are perceptible at multiple spatio-temporal scales and levels of ecological organization. The effects can be highly localized (*e.g.*, nests and vicinity) or extend throughout the habitat (*e.g.*, the foraging area), and influence individual plants, regenerating plant communities, and ecosystem functioning, including nutrient cycling. The impacts are persistent during the lifetime of colonies, but some effects can extend long after colony death or nest abandonment. Third, ecosystem-level effects from LCA activity are examples of ecosystem engineering that can alter the abundance of organisms by modifying patterns of coexistence and the successional trajectory of vegetation. Fourth, the effects induced by

LCA activities are context-dependent, species-specific, and modulated by anthropogenic activities. The challenge now is how to quantify these LCA-driven effects.

NEW DIMENSIONS TO THE ECOLOGICAL ROLES OF LCA ACROSS THE CHANGING TROPICS

In coming decades, the growth and spread of the human populations in tropical countries will result in large tracts of forest being converted into archipelagos of fragments and regenerating forest patches (Wright 2005). With the expansion of agricultural frontiers, many small forest fragments within private landholdings are likely to be confined to economically marginal lands and become gradually embedded in a human-managed, harsh matrix dominated by pastures, croplands, and urban areas (Tabarelli *et al.* 2004). These sort of anthropogenic and highly fragmented agro-mosaics are already the predominant landscape across many previously forested tropical lands (Harvey *et al.* 2008, Melo *et al.* 2013).

In this ecological context, some LCA species are able to permanently increase colony density up to 20 times (Meyer *et al.* 2009, Dohm *et al.* 2011). In fact, these insects are probably among the most ‘successful’ species in anthropogenically modified tropical landscapes (Wirth *et al.* 2007, Tabarelli *et al.* 2012a). LCA, especially of *Atta*, proliferate in modified habitats such as pastures (Fowler 1983), plantations (Oliveira *et al.* 1998), forest

remnants (Rao *et al.* 2001, Terborgh *et al.* 2001), edges (Wirth *et al.* 2007, Meyer *et al.* 2009, Dohm *et al.* 2011, Carvalho *et al.* 2012), secondary forests (Haines *et al.* 1990, Vasconcelos & Cherrert 1995, Silva *et al.* 2009), and roadsides (Vasconcelos *et al.* 2006). In recent years, there have been major advances in our understanding of the causal relationships behind this phenomenon, although it remains to see how general the mechanisms are (see Vasconcelos 1988, van Gils *et al.* 2011, van Gils 2012, van Gils & Vanderwoude 2012). Apart from the increased availability of suitable nesting-sites (Vasconcelos 1990, Vieira-Neto & Vasconcelos 2010), other explanations involve the relaxation of both top-down and bottom-up population controls (Terborgh *et al.* 2001, Urbas *et al.* 2007, Almeida *et al.* 2008, Wirth *et al.* 2008, Falcão *et al.* 2011). In disturbed areas, colonies suffer less attacks by predators (Wirth *et al.* 2008) and parasitoid phorid flies (Almeida *et al.* 2008) than in non-disturbed areas. There are also more pioneer species (Laurance *et al.* 2006, Santos *et al.* 2008) that are preferred by LCA (Farji-Brener 2001, Wirth *et al.* 2003, Falcão *et al.* 2011).

Such increased abundance of LCA fundamentally alters their impact as herbivores and ecosystem engineers in disturbed areas. For example, reports on forest area-based herbivory rates vary from 2.1 percent of the available foliage area in an undisturbed late successional forest in Panama (0.52 *Atta colombica* colonies/ha, Herz *et al.* 2007) to 36 percent on the edge of human-modified Atlantic forest (2.79 *A. cephalotes* colonies/ha, Wirth *et al.*

2007, Urbas *et al.* 2007, Meyer *et al.* 2009). The latter value greatly exceeds the overall rate of herbivory estimated for tropical forests (5–15%, Schowalter *et al.* 1986, Landsberg & Ohmart 1989, Coley & Barone 1996). Similarly, *A. cephalotes* nests increase light levels in approximately 0.6 percent of the interior of patches of Atlantic forest, but up to 6 percent of the area along forest edges where colonies are aggregated (Meyer *et al.* 2011a). Even more striking, the nest-driven decline in litter cover and nutrient status of topsoil layers, usually a local phenomenon spanning *ca* 0.6 ha per colony, was estimated to affect the entire forest edge (Meyer *et al.* 2013). All of these factors can help create a feedback between forest fragmentation and disturbance, LCA abundance, and plant community structure that promotes greater ant abundance and favors pioneer species (Fig. 5).

The pathways we propose for how LCA influence Neotropical ecosystems are working hypotheses, and we suggest future research should examine the generality of both patterns and the explanatory mechanisms proposed with cross-taxa and cross-ecosystem comparisons. Other ‘knowledge gaps’ include the traits making LCA successful in disturbed areas, the nature of novel, emergent or transition ecosystems resulting from the proliferation of LCA, cascades—particularly trophic cascades—mediated by LCA-driven vegetation shifts, the impacts of inactive nests on plants, and the mechanisms behind soil depletion around active ant nests and the fate of nutrients deposited into subterranean refuse chambers.

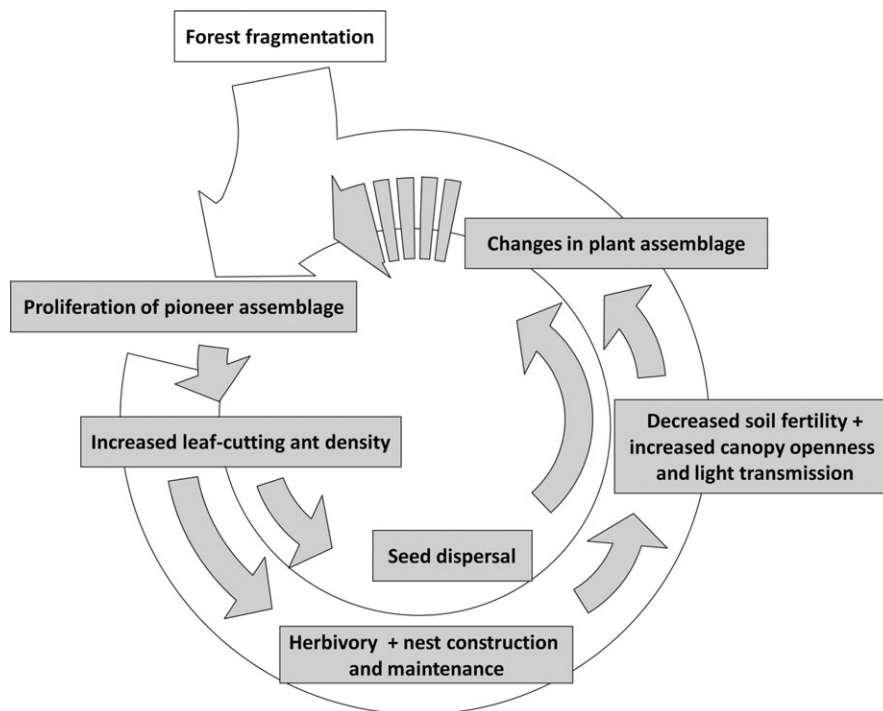


FIGURE 5. Synergism between forest fragmentation and leaf-cutting ants (modified from Meyer 2008). Forest fragmentation promotes proliferation of pioneers, sustaining a higher LCA colony density. Leaf-cutting ants in turn benefit pioneer assemblages directly through their activity as seed dispersers and indirectly via herbivory and nest construction activities; they also create canopy openings. These illuminated habitats favor pioneer recruitment and thus promote a feedback between plant communities and ants.

A promising pathway for filling such knowledge gaps and linking them with potentially emerging roles played by LCA is to examine how LCA contribute to the large-scale patterns of vegetation dynamics in human-modified landscapes. Because they primarily interact with and benefit from pioneer plant species, it is likely that they either potentialize or mitigate processes such as persistence of secondary forests (Tabarelli *et al.* 2008). How? Forest edges promote pioneer proliferation, which supports higher colony density. Leaf-cutting ant activities in turn favor pioneer species directly via seed dispersal and indirectly by microclimatic alterations resulting from herbivory and nest construction and maintenance (Fig 5). LCA therefore amplify environmental homogeneity and favor early successional systems. This working hypothesis of a detrimental anthropogenic-biogenic synergism contrasts with the traditional view of LCA as ecosystem engineers that promoting environmental heterogeneity and increased species diversity (Wirth *et al.* 2003). By creating long-term mosaics of soil and light regimes (see Corrêa *et al.* 2010, Bieber *et al.* 2011, Meyer *et al.* 2011a,b, 2013), LCA may favor species coexistence and diversity (via pioneer control and favoring niche partitioning) across disturbed habitats, which without LCA would be progressively dominated by few disturbance-adapted species (Tabarelli *et al.* 2012a).

Finally, our understanding of LCA effects would be greatly advanced by exclusion-based experiments. Despite a wealth of valuable insights from correlative fieldwork, multifactoriality and interactions among individual positive and negative LCA effects make drawing novel conclusions on LCA impacts a challenge. Note that such novel ecological roles for LCA as promoters of heterogeneity or homogeneity are far from negligible—by promoting either heterogeneity or homogeneity, leaf-cutting ants operate not only as agricultural pests but also as key ecological key players in human-modified landscapes.

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