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Leaf-cutting ants revisited: Towards rational management and control

James Montoya-Lerma^{a*}, Carolina Giraldo-Echeverri^b, Inge Armbrrecht^a, Alejandro Farji-Brener^c and Zoraida Calle^b

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Leaf-cutting ants, being the principal herbivores and ecosystem engineers in the Neotropics, have been considered to be a keystone species in natural ecosystems and agroecosystems, due to the direct and indirect effects of their plant defoliation activities. This review summarizes current concepts of the biological and ecological importance of leaf-cutting ants. The ants' pest status is briefly assessed from both ecological and evolutionary points of view. A general overview of control measures is provided. Leaf-cutting ants have evolved physical, symbiotic and behavioural mechanisms that allow them to overcome the chemical, biological, mechanical and cultural methods that have been used to manage their populations. Given the highly complex ecology of these ants, simple methods of control should not be expected. Sound management strategies must alternate between, and combine, different methods.

Keywords: *Acromyrmex*; *Atta*; biological control; chemical control; ecological importance; pest

1. Introduction

Species of *Atta* and *Acromyrmex* (Formicidae: Myrmicinae) are well known as leaf-cutting ants. They have a mutualistic relationship with basidiomycete fungi belonging to two genera, *Leucoagaricus* and *Leucocoprinus* (Agaricaceae: Leucocoprinae) (Mueller et al. 2001). Leaf-cutting ants (hereafter, termed LC ants) are key organisms in most neotropical ecosystems. Their activities as herbivores and soil-modifiers have major environmental effects in natural ecosystems (Holl Dobler and Wilson 2011). However, a contrasting scenario occurs in human-inhabited areas, where some LC ant species appear to take advantage of anthropogenic landscape alterations and become some of the most problematic pests in neotropical agricultural and pastoral systems (Blanton and Ewel 1985).

It is thus necessary to understand the responses of LC ant species to anthropogenic stresses, and to discriminate between (a) the response to human intervention, and (b) responses to climatic changes and episodic events at various spatial and temporal scales. It is also important to be able to define proper economic damage thresholds. Perhaps the most challenging issue regarding LC ants is the pest problem's complexity and multidimensional nature, and the interdisciplinary approach required, involving biologists and socioeconomic scientists. This overall challenge requires basic knowledge of, though not exclusively, ecology (from microbiology to landscape ecology), entomology, agronomy, sociology and

economics. Although an extensive literature has grown in relation to some of these topics, much of it is scattered and unavailable to the scientific community. This review is intended to update current knowledge regarding the economic impact and control of LC ants in neotropical areas.

We begin by discussing general concepts concerning the biological and ecological importance of LC ants. A brief assessment of pest status follows in the section on ecological and evolutionary points of view. Next, we provide a synoptic presentation, contextualized within the affected agricultural systems, of the main LC ant pest species; special emphasis is placed on the discrete but substantial role of some ant species as potential urban pests. Finally, after a general overview of the control measures used, an innovative integrated management strategy is proposed.

Although we focused mostly on published peer-reviewed literature, in some instances, information was supplemented by the authors' experience and data gathered from academic documents such as unpublished master and doctoral theses. Also, in a few cases, when merited and considered reliable, "grey" literature (e.g. proceedings from congresses) was used.

2. Leaf-cutting ants biology and fungus gardening

Atta and *Acromyrmex* are phylogenetically derived genera of a monophyletic group that is involved in mutualism with basidiomycete fungi belonging to two

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genera, *Leucoagaricus* and *Leucocoprinus* (Agaricaceae: Leucocoprinae). In this ancient interaction, which arose about 30 million years BP (Holldobler and Wilson 2011), freshly-cut plant material is used to culture the fungal gongylium which serves as the main source of food for ant colonies (Mueller et al. 1998, 2001; Bacci et al. 2008). The fungus is dispersed during the ants' nuptial flight (Scott et al. 2010).

Fungal transmission occurs vertically, that is, the fungus depends on the ant both for its clonal propagation within each colony and for the formation of new colonies. However, some studies report that, occasionally, there may be lateral transfer of inoculum of the fungus colonies of sympatric species (Mueller et al. 2011). In general, the fungus grows from the existing garden at the maternal colony (Mueller et al. 2001). Before departing from the maternal colony, each new queen carries fragments (pellets) of the symbiotic fungus in her infrabuccal pocket. After nuptial mating, the foundress queen spits out the mycelial wads and starts the garden in her colony (Schultz 1999; Santos et al. 2004). Ant workers forage for fresh leaves, not for direct consumption but in order to degrade them, forming a macerated pulp which serves as the substrate for cultivation of the fungus (Schultz 1999). *Atta* and *Acromyrmex* can be regarded as the most complex and efficient biological systems in which leafcutter agriculture has evolved (Schiøtt et al. 2010).

3. Ecological importance

3.1. Leaf-cutting ants as ecosystem engineers

Leaf-cutting ants have been regarded as keystone species (Fowler et al. 1989; Perfecto and Vandermeer 1993) and, latterly, as ecosystem engineers (Folgarait 1998; Wirth et al. 2003; Rico-Gray and Oliveira 2007; Farji-Brener et al. 2010) based on the disturbances they cause in tropical forests (Farji-Brener and Illes 2000; Meyer 2008). The abundance (numbers and biomass) of some species of LC ants greatly affects diversity, productivity, nutrient and energy flows, thus supporting their nomination as keystone species (Fowler et al. 1989; Schowalter 2011). Jones et al. (1994, 1997) define ecosystem engineers as organisms that directly or indirectly modulate the availability of resources for other species by causing physical state changes in biotic or abiotic materials. In doing so, they modify, maintain and/or create habitats (Jones et al. 1994, 1997).

3.2. Effects of leaf-cutting ants on soil fertility

Different studies have shown: (1) positive effects of LC ants on soil characteristics (Alvarado et al. 1981; Farji-Brener and Silva 1995; Farji-Brener and Medina 2000; Moutinho et al. 2003); (2) higher concentrations of macronutrients and improved soil penetrability in ant nests compared with non-nest soils (Haines 1975, 1983; Farji-Brener and Silva 1995; Moutinho et al. 2003);

(3) higher nutrient availability for plants in ant-nest refuse chambers (Haines 1975, 1983; Farji-Brener and Ghermandi 2000, 2004, 2008; Moutinho et al. 2003); (4) direct nutrient uptake by plants neighbouring ant nests (Sternberg et al. 2007; Farji-Brener and Ghermandi 2008).

The soil beneath the nests of *Atta cephalotes* Latreille. (0–2 m depth) in Costa Rica had a lower density and higher porosity than neighbouring soils (Alvarado et al. 1981). Soil nutrient concentrations were higher beneath soil-surface refuse piles (0–20 cm of soil depth) of *A. colombica* (Guérin-Méneville), where root density was also higher (Haines 1975, 1978). The same was true for nests of *A. laevigata* (Smith) (0–20 cm depth) in Venezuela (Farji-Brener and Silva 1995).

In a secondary forest of the Amazon, *A. sexdens* L. modified the soil surrounding their nest chambers, causing a decline in resistance to penetration, increased concentrations of plant nutrients and significant root proliferation within the soil associated with the nests (Moutinho et al. 2003). The soil underneath *A. sexdens* nests at different depths (100, 200, and 300 cm) showed low (five-fold) resistance to penetration (due to soil compaction) and was richer in Ca (3–4-fold), K (7–14-fold), Mg (2–3-fold) and P (1.5–2.0-fold) when compared with non-nest soil (Moutinho et al. 2003). The changes in nest soil properties were accompanied by increased coarse and fine root biomass (>2 mm diameter, 3–4-fold; <2 mm diameter, 10–50-fold, respectively). These results extended the known influence of LC ant nests in deep soil horizons (2–3 m), indicating that some species play a key role in bioturbation, altering the properties of massive soil volumes (Moutinho et al. 2003).

Sternberg et al. (2007) offered leaves labelled with the stable isotope ^{15}N to two species of LC ants (*A. colombica* and *A. laevigata*) at a moist tropical forest site in Panama and a savannah site in Brazil. The stable isotope label was detected in plants surrounding the nests of both ant species. Leaf tissue of trees located near the nests labelled with ^{15}N had significantly higher calcium concentrations than those of distant, unlabelled conspecifics. Calcium is known to be a limiting macronutrient in tropical forests and savannahs. The aforementioned observations support the idea that LC ants concentrate and supply critical macronutrients to plants (Sternberg et al. 2007). Bueno et al. (2007) studied the chemical composition of the refuse material produced by laboratory colonies of LC ants fed with two plant substrates. Nutrient concentration in the refuse material was consistently higher than in leaves of both plant species: the refuse material was enriched by nutrients from ant carcasses, fungal activity and excretions (Bueno et al. 2007).

Leaf-cutting ant nests (mainly *Acromyrmex* spp.) affect temperate ecosystems, where they enrich soil, modify vegetation patterns and function as refuges for

rare plant species, particularly during high water stress periods (Farji-Brener and Ghermandi 2000, 2004, 2008). *Acromyrmex lobicornis* Emery, the only LC ant species found in the arid region of Patagonia, places its refuse material on the soil surface where it is accessible to plants and seeds. Tadey and Farji-Brener (2007) found a higher content of N, C and P in refuse dumps than in adjacent non-nest soils. However, the strength of this effect decreased with cattle grazing pressure; as stocking rate increased, the nutrient content of the refuse dumps decreased.

3.3. Abandoned leaf-cutting ants' nests as distinct habitats

Large and long-lived nests of LC ants have various positive ecological effects in tropical and subtropical forests (Farji-Brener and Illes 2000): (1) Increased light incidence at ground level by maintaining open areas. This can favour small-seeded plant species requiring more light for establishment and early growth. (2) Increased availability of unoccupied ground through litter removal (Weber 1982). This can favour species requiring bare soil for germination and establishment. (3) Altered physical properties of soils, that is, enhanced soil porosity and penetrability (Moutinho et al. 2003). (4) Altered chemical properties of soils through accelerated nutrient cycling in the nest area. (5) Changes in vegetation dynamics. In savannas and open woodlands of Paraguay and Argentina, abandoned *Atta vollenweideri* (Forel) nests are colonized by *Prosopis* spp. trees. Ant nests are safe sites for these seedlings because they are free of grasses, richer in nutrients and have greater amount of soil water (Jonkman 1978; Bucher 1982). *Atta laevigata* favours the establishment of *Tapirira velutinifolia* (Cowan) Marcano-Berti (Anacardiaceae) in the savannas of Venezuela by removing pulp from seeds, thus preventing infection by pathogens and enhancing the recruitment of this species (Farji-Brener and Silva 1996). (6) Landscape-level effects: formation of woody islands in open habitats (Jonkman 1978; Farji-Brener and Silva 1995). (7) Fruit and seed collection and carrying; these activities concentrate individuals of specific plant species in the nutrient-rich nest area. (8) Active nests differ from abandoned ones in their effects on understory plant abundance and species richness in Costa Rica (Garretson et al. 1998; Farji-Brener 2005). While active nests have fewer seedlings and fewer species than surrounding soil, abandoned nests have 73% more individuals and 58% more species. (9) *Atta* nests can increase fine-scale spatial heterogeneity in some ecosystems by altering the performance of certain plants. Wirth et al. (2003) found that an increase in resource heterogeneity in a Panamanian rain forest was the result of a variably (patchy) distributed increase in light availability and nutrient concentrations. A suite of microclimatic effects resulted from the altered forest

structure at nest sites of *A. cephalotes*. Even though nests are small-scale disturbances, their microclimatic effects extend several metres into the surrounding forest, increasing the area affected per nest. Nest excavation and agricultural activities of *A. sexdens* create complex below-ground heterogeneity in secondary forests of eastern Amazonia (Verchot et al. 2003). Nests create "bottom-up" gaps in forests (Farji-Brener and Illes 2000; Hull-Sanders and Howard 2003). These openings, which originate in the understory, have their most important effects through soil disturbance, 2 m below the ground (Alvarado et al. 1981; Perfecto and Vandermeer 1993). The effects of enhanced plant size and quality in LC ant refuse dumps can spread to organisms at higher trophic levels, such as aphids and aphid-tending ants. In the Patagonian desert steppe, individuals of the thistle species *Carduus nutans* L. and *Onopordum acanthium* L. that had become established in ant refuse dumps of *Acromyrmex lobicornis* showed 100–300% more leaves and inflorescences and 100% more foliar N than those established in non-nest soils. In *C. nutans*, the enhanced plant size and quality were associated with an increase in the relative abundance of aphids. Accordingly, the number of ant species that tended aphids increased per individual plant in refuse dump plants in these thistle species (Farji-Brener et al. 2009). (10) LC ant nests provide nesting sites for other vertebrate and invertebrate species while the ants themselves are food resources for certain species. Reptiles use *Atta* nests as egg-laying sites (Azevedo-Ramos and Moutinho 1994). Inseminated winged *A. laevigata* ants are used as oviposition sites by the dung beetle *Canthon virens* Mannerheim in the Brazilian Cerrado (Hertel and Colli 1998). Dung beetles have been observed to decapitate and then bury their much larger ant victims as part of a specialized and probably obligatory predatory behaviour (Hertel and Colli 1998).

3.4. Leaf-cutting ants as ecological filters

Ecological filters are important in selecting species from potential species pools (Keddy 1992; *sensu* Geho et al. 2007; Meyer 2008). LC ants can act as ecological filters by modifying succession through substrate alterations and by affecting seed dispersal patterns.

3.5. Leaf-cutting ants' effects on succession

LC ant nests have been considered a major disturbance in neotropical soils (Alvarado et al. 1981), given that they concentrate cut-leaf biomass, creating enriched soil patches (Haines 1975, 1978) and thus induce particular patterns of associated vegetation (Fowler 1977; Farji-Brener and Silva 1995). Therefore, it has been suggested that selective grazing, leaf concentration and soil enrichment by LC ants may be important factors determining patterns of succession (Cherrett

1989; Nichols-Orians 1991; Farji-Brener and Silva 1995; Vasconcelos 1997; Vasconcelos and Cherrett 1997; Farji-Brener and Medina 2000; Farji-Brener and Illes 2000; Rico-Gray and Oliveira 2007). Garretson et al. (1998) found a reduced diversity and abundance of understory plants in the area around active nests of *A. cephalotes*, and a larger diversity and abundance of small understory plants in abandoned nests in Costa Rica. In north-eastern Brazil, nests abandoned by *A. cephalotes* exhibited less dense, impoverished and more homogeneous regenerating plant assemblages than surrounding areas at local and landscape scales. Both studies showed a transient population recruitment bottleneck. Thus, it seems that, under certain conditions, abandoned nests represent relatively long-lasting (even 15 years) islands of unsuitable substrate that reduce plant recruitment, retard forest regeneration, and fail to provide a (special) regeneration niche able to promote species coexistence and plant diversity (Bieber et al. 2011).

3.6. Leaf-cutting ants and seed dispersal

The effects of LC ants on seed dispersal and germination have been studied by Oliveira et al. (1995); Farji-Brener and Silva (1996); Nascimento and Proctor (1996); Dalling and Wirth (1998), Leal and Oliveira (1998), and Farji-Brener and Medina (2000). The activity of these ants can have a positive effect on plant fitness when they remove seeds and fruits from the forest floor (Alvarez Buylla and Martínez-Ramos 1990; Kaspari 1996; Leal and Oliveira 1998, 2000). Seed removal and relocation by LC ants might be sufficient to affect local recruitment patterns of trees: *Mycocephurus goeldii* Forel (Attini) facilitates the germination of *Hymenaea courbaril* L. (Caesalpinaceae) (Oliveira et al. 1995); *Acromyrmex striatus* (Roger) disperses the seeds of *Schinus fasciculatus* (Anacardiaceae) in the dry Chaco shrubland of Argentina (Varela and Perera 2003); *Atta laevigata* contributes to the establishment success of *Tapiria velutinifolia* (Farji-Brener and Silva 1996), and *A. colombica* aids in the seed dispersal of *Miconia argentea* (Sw.) Dc. (Melastomataceae) (Dalling and Wirth 1998). In the Brazilian savanna, most fallen *Miconia rubiginosa* fruits are removed by ants. Seedlings and saplings of *Miconia* are frequently found around LC ant nests. These ants probably reshape the seed “rain” generated by primary dispersers by removing seeds from bird droppings and recovering seeds that fall under parent trees (Christianini and Oliveira 2010). However, attine LC ants such as *A. cephalotes*, *Trachymyrmex* sp. (Nascimento and Proctor) and *Sericomyrmex aztecus* (Kaspari) act as seed predators when they remove the seeds of *Peltogyne gracilipes* Ducke (Caesalpinaceae) and *Miconia affinis* Dc. (Melastomataceae), respectively, and transform them into a fungus-growing substrate (Rico-Gray and

Oliveira 2007). Silva et al. (2007) found that *A. sexdens* collected approximately 20% of the seed crop of the non-myrmecorous *Protium heptaphyllum* (Aubl.) Marchand (Burseraceae) in the Atlantic forest of Brazil. This promoted short-distance dispersal, high levels of seed aggregation and greatly reduced rates of seedling survival (Silva et al. 2007).

4. Why do leaf-cutting ants become pests?

Considering the multiple ecological roles that LC ants play in natural ecosystems, it is useful to ask why they have become pests in anthropogenic environments. The answer is likely to invoke multiple ecological mechanisms. In natural environments, bottom-up and top-down forces preclude the proliferation of a given species. However, there is an urgent need to understand the ecological mechanisms that underlie the distribution of LC ants, their abundance and dispersal (Camargo et al. 2006).

In cultivated systems, the use of chemical fertilizers can promote and increase the attack of leaf-cutting ants because they prefer plants that have high concentrations of foliar nitrogen (N) and phosphorus (P), both of which favour the growth of symbiotic fungi, and low levels of iron (Fe), manganese (Mn) and aluminium (Al), which alter their growth (Berish 1986). Nichols-Orians (1991) found that in open areas, fertilized plants of *Piper arieianum* Steyererm were more prone to herbivory by *A. cephalotes* than unfertilized ones. Similarly, Giraldo-Echeverri (2005) found a higher level of *A. cephalotes* herbivory causing a severe alteration of tree architecture in plantations of *Montanoa quadrangularis* Schultz Bipontianus (Asteraceae) fertilized with chemicals than in similar trees mulched with the Mexican sunflower, *Tithonia diversifolia* (Helmsl.) Gray (Asteraceae). One factor that may favour the increase of LC ant populations in cultivated systems is related to the intrinsic preference of LC ants for some plant species in natural ecosystems. It would be worth exploring whether LC ants in the Americas were pre-adapted to becoming serious pests following the introduction of defenceless domesticated/cultivated plants.

Another life-history trait that may predispose certain LC ants to becoming pests is the lack of aggressiveness among conspecifics, related to the absence of a colony-specific odour. This might explain the high probability of establishment and success, leading to high densities of LC ants in certain areas (Leal and Oliveira 1998; de Souza et al. 2006), where LC ants take advantage of human landscape alterations, such as agriculture and urbanization.

Finally, LC ants queens prefer nesting in open areas rather than in closed forest (Vasconcelos 1997). Therefore, the clearing practice that precedes the conversion of forests to cultivated lands may favour an exaggerated proliferation of LC ants.

4.1. Leaf-cutting ants as agricultural pests

Almost any LC ant species fulfills the broad definition of a (plant) pest given by the Food and Agriculture Organization (FAO 2010): “any species, strain or biotype of plant, animal or pathogenic agent injurious to plants or plant products”. Farmers and human communities often perceive LC ants as serious pests wherever they are present (Serna and Correa 2003). This issue deserves special attention as LC ants are indiscriminately controlled by farmers despite the fact that the majority of ant species are not actual pests, but endemic and geographically restricted (Fowler et al. 1989). However, information on the magnitude of the damage and economic harm caused by LC ants is levels is mostly lacking (Della Lucia 2003). In the absence of a precise definition for species of LC ant acting as agricultural pests, we offer the following: “a leaf-cutting ant species is a pest when its presence and abundance threatens the return of, or the profit of, an investment on a farm by decreasing the quantity and/or quality of an agricultural product”. LC ant species are assigned to a given category based on their geographical distribution, the number of crop species affected and the reports of crop damage in the countries ($n = 21$) as listed in Table 1. Consequently, a LC ant species is considered to be a primary pest if it is present and reported as a crop pest in $\geq 80\%$ of countries. A LC ant species would be considered a secondary pest if present and reported in 21–79% of the countries studied, and a tertiary pest if present and recorded in 1–20% of countries. After a strict revision, only 5 out of 37 LC ants listed in Fowler et al. (1989) can now be considered to be primary pests (Table 1).

The relatively small number of herbivore species acquiring pest status is probably due to the fact that wide polyphagy is unusual among tropical herbivores (Janzen 1981). However, few attempts have been made to quantify economic thresholds of LC ant herbivory due to the inherent difficulty of manipulating populations and the unpredictability of ant attacks on plants. A cheap and easy method to measure herbivory rates by LC ants was developed for *A. colombica* by estimating the number of refuse fragments deposited in the refuse piles each day (Herz et al. 2007). However, this can only be done with LC ant species that deposit refuse material outside their nests.

Yet another problem in determining pest status is the “difficult” taxonomy of LC ants: it is not straightforward and is far from being resolved. There is consensus that *Atta* and *Acromyrmex* are the most evolved genera of the higher Attini, the monophyletic group formed by fungus-growing ants (Mueller et al. 2001; Schultz and Brady 2008). Both of them are diverse and include many species that show a high degree of morphological plasticity (Mayhé-Nunes 2002). Although there are only 15 recorded *Atta* species and 35 of *Acromyrmex*, both taxa harbour many subspecies. The most complete species list is

available online (<http://www.discoverlife.org/mp/20q?search=Atta>).

The geographic distribution of *Atta* and *Acromyrmex* is usually restricted by altitude (< 1900 m.a.s.l.) and latitude, between 33°N and 44°S (Lofgren and Vander Meer 1986; Farji-Brener and Ruggiero 1994), though Carrasco (1962) observed LC ants at 2040 m in Peru. Despite their wide distribution and wide potential to attack flowering plants, the vast majority of LC ants are surprisingly harmless (Table 1). In the first group primary pests are *A. cephalotes*, *A. sexdens* and *A. laevigata*, *Ac. octospinosus* and *Ac. balzani* Emery, *Ac. rugosus* Smith and *Ac. brunneus subterraneus* Forel, which, under certain circumstances, reach population densities capable of defoliating all green plants in the ants’ home range (Della Lucia 2003; Byrne 2004). However, this situation varies according to geographic area, vegetation type and various environmental factors. Global economic losses due to LC ants are based on questionable estimates, but it is accepted that the “rough” estimate given by Hölldobler and Wilson (1990), based on the work of several authors (Table 2), that the losses are in the order of billions of dollars (US\$) is still very conservative. It is difficult to establish a valid threshold, as ant communities behave as one “superorganism” and there is no standard technique adequate for all species, places and conditions.

4.2. Food preferences and specialization

Selection of host plants (i.e. leaf tenderness, nutritional contents, and absence of deleterious metabolites) by worker ants is a crucial issue. Actually, this determines leaf quality which, in turn, influences the recruitment and harvesting in the ant colony. Although some species such as *Ac. octospinosus* and *Ac. volcanus* Wheeler scavenge for pieces of fallen vegetation such as dead leaves, flowers or fruits, in addition to cutting herbs (Wetterer 1995), the substrates preferred by LC ants are newly formed leaves, tissues with high moisture and nutrient contents, and also leaves of crop plants. Mature leaves have fibrous tissues with higher concentrations of lignin and structural carbohydrates that are difficult for the ants to cut and digest. This, coupled with lower nutritional quality (Howard et al. 1988) and the presence of secondary metabolites including phenols, alkaloids, terpenes, tannins and other chemical plant components, are deleterious to the mutualistic fungus. Plant selection is important for ants because many of the minor components of plants affect the fungus. Ants tend to avoid leaves with components having antimicrobial properties (e.g. phenols) or those that determine plant resistance to ant attack (Levin 1976; Hubbell et al. 1984).

All of the aforementioned factors explain why relatively few species of LC ants (such as *A. cephalotes*, *A. sexdens* and *A. laevigata*, as well as *Ac. balzani*, *Ac. rugosus* and *Ac. brunneus subterraneus*) are important

Table 1. *Atta* and *Acromyrmex* species considered as pests in different agricultural crops in the Americas.

Leaf-cutting ant species	Altitude and median altitude (m.a.) (m)	Geographical distribution (countries and [%])	Host preference and additional information	Impact as pest	References
<i>Atta cephalotes</i>	5–1500 meters (m.a. 356 m)	Ant, Barb, Bel, Bra, Bol, Col, Cr, Ecu, FG, G, Guat, Hond, Mex, Nic, Pan, Per, Sur, T&T, Ven, and W. Ind (79.2)	Cocoa, citrus, coffee, cotton, maize, cassava. A list of the plants associated with coffee plantations and harvested by this ant species is presented in Varón et al. (2007). <i>Piper aricanum</i> , <i>Montanoa quadrangularis</i> , <i>Vochysia guatemalensis</i> , <i>Hyeronima alchorneoides</i> . Fajri-Brener (2001), based on reviewed literature, provides a list of forest plant species foraged by this species	Very wide	Ant Web (2011); Bieber et al. (2011); Meyer et al. (2011); Garen et al. (2009); del Toro et al. (2009); Ortiz and Guzmán (2007); Giraldo-Echeverri (2005); Byrne (2004); Oliveira et al. (2004); Urbas (2004); Fajri-Brener (2001); Laurance et al. (1998); Nichols-Orians (1991); Vasconcelos (1990); Jaffé and Vilela (1989); Nichols-Orians and Schultz (1986); Blanton and Ewel (1985); Korytkowski and Aguilar (1980); Rockwood (1976); Cherret (1968); Carrasco (1962)
<i>Atta sexdens</i>	100–450 meters (m.a. 170 m)	Arg, Bol, Bra, Col, Par, and Ven (25.0)	In Venezuela it causes defoliation in cassava, <i>Eucalyptus grandis</i> Hill ex Maiden, <i>Pinus elliottii</i> , <i>P. taeda</i> L., <i>P. caribaea</i> Mor. This ant forages opportunistically, simultaneously using trees and a wide variety of (ephemeral) resources including seedlings, juveniles, flowers and dead leaves from ground litter. It has been overseen attacking a wide range of crops at altitudes up to 2040 m, Mador Pampa, Peru. Trees of <i>Clitoria fairchildiana</i> R. Howard (Fabaceae), <i>Anacardium occidentale</i> L. and <i>Schinus terebinthifolius</i> Raddi (Anacardiaceae)	Wide	Poderoso et al. (2009); Ortiz and Guzmán (2007); Bertorelli et al. (2006); Della Lucia (2003); Teixeira et al. (2003); Vasconcelos (1990); Araujo et al. (1997); Fowler et al. (1996); Lapointe et al. (1996); Carrasco (1962)
<i>Atta laevigata</i>	n/a	Bra, Col, G, Par, and Ven (20.9)	<i>Eucalyptus</i> , <i>P. caribaea</i> , sylvatic or savannas. Trees of <i>C. fairchildiana</i> , <i>A. occidentale</i> and <i>S. terebinthifolius</i>	Wide	Poderoso et al. (2009); Ortiz and Guzmán (2007); Hernández and Jaffé (1995); Hernández et al. (1999); Araujo et al. (1997); Fajri-Brener (1993); Salzemann and Jaffé (1990); Cherret (1986)
<i>Atta capiguara</i> Gonçalves	n/a	Bra and Par (8.3)	Grasses	Narrow	Fowler (1985)
<i>Atta bisperica</i> Forel	n/a	Bra (4.1)	Gramineous, sugar cane (<i>Sacharum officinalis</i> L.)	Narrow	Della Lucia (2003)
<i>Atta mexicana</i> Smith	530–1990 meters (m.a. 1201 m)	ES, Gua, Hon, Mex, and USA (20.9)	Coniferous. Nest at base of saguaro (<i>Carnegiea gigantea</i> Englem) and cholla cacti	Wide	Wild (2003); Rojas and Fragoso (2000); Mintzer (1979)

(continued)

Table 1. (Continued).

Leaf-cutting ant species	Altitude and median altitude (m.a.) (m)	Geographical distribution (countries and [%])	Host preference and additional information	Impact as pest	References
<i>Atta Texana</i> (Buckley)	30–260 meters (m.a. 128 m)	Mex and USA (8.3)	A serious pest in planted pines (<i>P. taeda</i>) especially during the winter season when, in the absence of grasses and weeds, it defoliates pine seedlings	Narrow	Kulhavy et al. (2001); Rojas and Frago (2000)
<i>Atta colombica</i>	10–500 m (m.a. 158 m)	Col, CR, Nic, Pan, and Per (20.9)	Wirth et al. (2007) did a census of forest plant species foraged by this species and Farji-Brener (2001) complemented it.	Wide	Ortiz and Guzmán (2007); Wirth et al. (2007); Sheperd (1985)
<i>Atta insularis</i> Güerin	n/a	Cub (4.1)	<i>Alchornea latyfolia</i> Sw., <i>Bauhinia cumananensis</i> Kunth <i>Chamissoa altissima</i> (Jacq.) Kunth, <i>Cissampelos pareira</i> L., <i>Cissus caustica</i> Tussac, <i>Gonzalagunia sagreana</i> Urb., <i>Hibiscus elatus</i> Swartz, <i>Nectandra antillana</i> Meins, <i>Piper aduncum</i> L., <i>Trema micrantha</i> (L.) Blume, <i>Vigna luteola</i> (L.) Kuntze	Narrow	Pintera (1983)
<i>Atta vollenweideri</i>	124 m	Arg, Par, and probably Per (12.5)	Grasses	Narrow	Carrasco (1962)
<i>Acromyrmex (landolti) balzani</i> Emery	n/a	Bra, Col, and Par (12.5)	<i>Eucalyptus</i>	Narrow	Ortiz and Guzmán (2007); Araújo et al. (1997)
<i>Acromyrmex coronatus</i> (Fabricius)	550–2190 m (m.a. 1371 m)	Bra, Col, CR, Ecu, Hon, and Par (25.0)	Herbaceous plants	Wide	Ortiz and Guzmán (2007); Wetterer (1995) AntWeb (2011); Ortiz and Guzmán (2007)
<i>Acromyrmex rugosus</i> <i>Acromyrmex landolti</i> (Forel)	180 m	Col and Par (8.3) Arg, Bra, Col, G, and Ven (20.9)	scrub forest Dominant in <i>P. taeda</i> and <i>P. elliottii</i> plantations in La Plata, Argentina. <i>Paspalum notatum</i> Flugge (Poaceae), <i>Cynodon dactylon</i> L. (Poaceae) and flowers of <i>Richardia brasiliensis</i> Gomes (Rubeaceae). <i>Brachiaria</i> is highly resistant to this ant; in the grass <i>Panicum maximum</i> Jacq., <i>Brachiaria dictyoneura</i> Figari et De Not and <i>Andropogon gayanus</i> Kunth in Venezuela	Wide	Ortiz and Guzmán (2007); Poderoso et al. (2009); Cantarelli et al. (2006); Lapointe et al. (1996); Lapointe (1993); Rubio et al. (1975); Labrador et al. (1972)
<i>Acromyrmex octospinosus</i> (Reich)	50–930 m (m.a. 175 m)	Col, ES, Hon, Nic, and Mex (20.9)	<i>Borreria laevis</i> (Lam.) Griseb., <i>Senecioides cinerea</i> (L.) Kuntze ex Britton & P. Wilson, <i>Sida rhombifolia</i> L.	Wide	del Toro et al. (2009); Ortiz and Guzmán (2007)

Ant = Antilles, Arg = Argentina, Barb = Barbados, Bel = Belize, Bol = Bolivia, Bra = Brazil, Col = Colombia, CR = Costa Rica, Cub = Cuba, Ecu = Ecuador, ES = El Salvador, FG = French Guyana, Guat = Guatemala, G = Guyana, Hon = Honduras, Mex = Mexico, Nic = Nicaragua, Pan = Panama, Par = Paraguay, Sur = Surinam, T&T = Trinidad & Tobago, USA = United States of America, Ven = Venezuela, W. Ind = West Indies.

n/a = not available.

Table 2. Entomopathogenic (E) and antagonistic (A) fungi used for *Atta* and *Acromyrmex* control.

Target species	Pathogen	Type of assay	References
<i>Atta sexdens rubropilosa</i> Forel	<i>Metarhizium anisopliae</i> (Metsch.) Sorokin (E)	Field colonies	Lima et al. (1986)
	<i>M. anisopliae</i> (E), <i>Beauveria bassiana</i> (Balsamo) (E)	Mini-test	Jaccoud et al. (1999)
	<i>M. anisopliae</i> (E), <i>B. bassiana</i> (E)	Bioassays of laboratory	Santos et al. (2007)
<i>A. sexdens piriventris</i> Santschi	<i>M. anisopliae</i> (E), <i>B. bassiana</i> (E)	Bioassays of field and laboratory	da Silva and Diehl-Fleig (1988)
<i>Atta</i> sp. and <i>Acromyrmex</i> sp.	<i>M. anisopliae</i> (E), <i>B. bassiana</i> (E), <i>Trichoderma lignorum</i> (Tode) Harz (A)	Field colonies	Escobar et al. (2002)
<i>A. cephalotes</i>	<i>M. anisopliae</i> (E), <i>B. bassiana</i> (E), <i>Trichoderma viridae</i> Per. Ex. Fr. (A)	Bioassays of field and laboratory	López and Orduz (2003)
	<i>M. anisopliae</i> (E), <i>Paecilomyces</i> sp. (E), <i>Trichoderma</i> <i>hammatum</i> (Bonord.) Bainier (A)	Field colonies	Varón (2006)
<i>Atta sexdens rubropilosa</i>	<i>M. anisopliae</i> (E), <i>B. bassiana</i> (E)	Bioassays of laboratory	Alves and Sosa Gomez (1983)
<i>Acromyrmex</i> spp.	<i>B. bassiana</i> (E)	Field colonies	Diehl-Fleig et al. (1993)
<i>Atta colombica</i>	<i>T. hammatum</i> (A), <i>B. bassiana</i> (E)	Bioassays of laboratory	Banderas Galvinaz (2004)
<i>A. cephalotes</i>	<i>Trichoderma viride</i> (A)		López and Orduz (2003)
<i>A. cephalotes</i>	<i>T. lignorum</i> (A), <i>Gliocladium</i> sp.	<i>In vitro</i>	Ortiz and Orduz (2000)

defoliators in both natural habitats and cultivated crops. The high degree of polyphagy and adaptability of these LC ants enables them to attack a wide range of plant tissues and species, although they do not harvest all plant materials with the same intensity (Howard 1987; Howard et al. 1988; Farji-Brener 2001). It is known that each LC species shows a preference for a restricted number of plant species: Rockwood (1976) found that colonies of *A. colombica* and *A. cephalotes* chose only 31% and 22%, respectively, of the plants available in the Costa Rican dry forest. In addition, he found that the most abundant plants were not the most heavily harvested.

Because the distribution of LC ants is mainly neotropical, the most frequently attacked crops are coffee (*Coffea arabica* L.), cocoa (*Theobroma cacao* L.), citrus (*Citrus* spp.), cassava (*Manihot esculenta* Crantz), maize (*Zea mays* L.) and cotton (*Gossypium hirsutum* L.). However, native and introduced pasture grasses and plantations of species for soft-forest and silvopastoral purposes are also affected (Cherrett 1986; Moulart et al. 2002; Pérez et al. 2011). Studies of LC ants have an uneven geographic distribution, and the number of published papers does not necessarily reflect either the damage caused by, or the importance of, a given species. Most studies published several decades ago were conducted in Panama (Burd 1996; Herz et al. 2007) and Costa Rica (Rockwood 1976; Burd 2000) probably reflecting the availability of funding and research facilities. In recent years, research in Brazil, Argentina and other South American countries has become increasingly important.

4.2.1. Coffee and cocoa

Generally, on coffee farms, plants other than coffee trees are preferred by LC ants (Varón et al. 2007); however, some LC ant species have overcome the

defensive chemical mechanisms of coffee, becoming economically important in coffee crop cultures in Central and South America: Nicaragua, Costa Rica, and Colombia and Brazil, respectively (Cherrett and Peregrine 1976; Barreto et al. 1998; Varón et al. 2007). Damage to coffee by LC ants occurs when they defoliate bushes and their nests affect the roots of coffee shrubs. According to Varón et al. (2007), herbivory and damage to roots by a large *A. cephalotes* colony, killed 20 coffee bushes. This LC ant species is also present in Colombian coffee areas where farmers consider it a growing problem (R. García, pers. comm.). In Brazil, Barreto et al. (1998) reported the defoliation of coffee crops by *A. sexdens rubropilosa*, though Carrasco (1962) specifically noted that neither coffee nor plantains were attacked by *A. sexdens fuscata* (Santschi), one of the most important pests in the department of Cuzco, Peru.

In cocoa plantations, in Brazil, Trinidad and Tobago, LC ant species are considered problematic for distinct reasons. In Brazil, *A. cephalotes*, *A. sexdens* and *A. laevigata*, as well as *Ac. balzani*, *Ac. rugosus* and *Ac. brunneus subterraneus* cut off cocoa leaves, bark and small pods, especially of young plants (Delabie 1990; Delabie et al. 1993, 1997). In addition, *Ac. octospinosus*, the most abundant and noxious species of several economically important ants of shaded cocoa plantations in Trinidad and Tobago, attacks the flower buds (Lewis 1975). Nevertheless, in both situations, damage is normally limited to a small number of plants. Hence, the overall impact on cocoa plantations is minimal and to some extent beneficial, since these ants contribute to nutrient cycling on the cocoa farms as well as in forests (Moutinho et al. 2003).

Several attempts, though not rigorous, have been made to establish the economic impact of LC ants in coffee and cocoa crops. In Trinidad, Cherrett and Sims (1968) suggested annual losses of 4% of the crop value

(i.e. US\$160,000, roughly \$1,034,473, at today's dollar value) in cocoa plantations. Interestingly, for the same country, Lewis (1975) mentioned that in areas with high nest densities (up to 153 nests ha⁻¹) only a small mortality rate (6-17%) could be attributed to LC ant defoliation in an undisturbed field of a young cacao plantation, after the first year of planting.

4.2.2. Cassava

In a controlled field study in Venezuela in which both *A. sexdens* and *A. landolti* were present, only the former species was found to cause severe damage to cassava crops, specifically during the establishment phase (Bertorelli et al. 2006). Defoliation of the plants severely affected the yield (kg ha⁻¹). An overall reduction of 55% was estimated for crops not treated with insecticide. A significant reduction in root length was identified as the main factor in reducing the number of plants and the yield of roots (kg ha⁻¹) (Bertorelli et al. 2006). In rural areas of the Colombian Amazon, we observed (Armbrecht and Montoya-Lerma, pers. obs., 2008; 2009) that LC ants are powerfully attracted to cassava plants. This assertion was supported by indigenous people around these villages who frequently identified these ants as the most limiting pest for the small cassava plots. However, in a one-year experimental study in Costa Rica, *A. cephalotes* cut only 17 out of 332 plant species occurring around a cassava system (Blanton and Ewel 1985). Before the harvest, the cassava received two-thirds of all ant attacks with daily losses of 88 cm² leaf area for every square metre of ground area (equivalent to 0.3% of the available cassava leaf tissue per day). Perhaps Blanton and Ewel's (1985) most important finding was that *A. cephalotes* cut lower proportions of total leaf area in those ecological communities that had greater structural complexity, species richness and leaf area.

4.2.3. Sugar cane

In Brazil, *A. bisphaerica* is a widely distributed LC ant species adapted to cutting graminaceous plants. It may cause the loss of 3.6 metric tonnes of sugar cane (*Saccharum* spp.) each year (Della Lucia 2003). In a broad estimation, Della Lucia (2003) revealed that up to US \$ 60,000,000 per year might be lost, considering 0.5 LC ants nests per hectare cause losses of 3 tonnes ha⁻¹ and bearing in mind that Brazil cultivates a total of 4 million ha of sugar cane per year. In Valle del Cauca, Colombia, *A. cephalotes* nests are regarded as a serious problem for sugar cane production, yet there is not a single accurate quantification of their economic impact. Given that sugar cane production continues during periods of drought dependent on mechanical or pump irrigation, circumstantial evidence indicates that colonies of LC ants increase water infiltration, thereby

causing a significant loss of expensive irrigation water. This has important social, economic and environmental implications.

4.2.4. Oil palm

In Peru, Korytkowski and Aguilar (1980) reported that *A. cephalotes* was causing very severe damage to oil palm (*Elacis guineensis* Jacq.) and claimed that control was usually effective through baited pesticides and nest destruction.

4.2.5. Forestry

In several neotropical countries, LC ants are important limiting agents for forestry, especially in young plantations (Blanton and Ewel 1985; Cherrett 1986; Jaffé 1986; Vilela 1986; Fowler et al. 1986; Folgarait et al. 1996; Della Lucia 2003; Pérez et al. 2011) and pastures (Lapointe 1993; Serrano et al. 1993). These ants have been reported to defoliate between 14% and 50% of conifer seedlings in plantations in Brazil and Venezuela (Jaffé 1986; Vilela 1986; Antunes and Della Lucia 1999; Hernández et al. 1999; Cantarelli et al. 2008). Leaf-cutter damage to young trees (<6 months old) can cause a 32% reduction in height, 25% reduction in girth and up to a 60% loss in timber yield (Della Lucia 2003). Vilela (1986) reported that LC ant control was responsible for 75% of reforestation expenses in Brazil. Araújo et al. (1997) found that *A. sexdens* and *Ac. laticeps nigrosetotus* Forel displayed the highest densities among the 11 attinine species nesting within *Eucalyptus* forest plantations, which have been extensively studied for decades in Paraopeba (Minas Gerais, Brazil). Even though *Ac. laticeps nigrosetotus* was not listed as a major pest by Fowler et al. (1989), other authors have considered this ant to be an important nuisance in Brazilian *Eucalyptus* plantations (Marsaro et al. 2007). A single colony with a fungus volume close to 1.3 litres could defoliate the trees of a regenerating plantation in just 3.6 days. There are remarkable records of up to 30 *Atta* colonies ha⁻¹ (Ribeiro and Woessner 1979; Jaffé 1986) and up to 200 *Acromyrmex* colonies ha⁻¹ in Brazilian forest plantations (Cherrett 1989). Zanetti et al. (1999, 2000) found that a high nest density directly and negatively affects productivity in *Eucalyptus* plantations. It has been estimated that 30% of the total expenditure for 7 million hectares of eucalyptus forest plantations till the third harvest cycle was destined for LC ant control, reducing timber price by 7.4% (Alipio 1989, quoted by Della Lucia 2003). A recent account reveals that *Acromyrmex* spp. occupy 98% of the nests of leaf-cutting ants in areas of *Pinus* sp. plantations (Cantarrelli et al. 2006), and that LC ant control may involve up to 5% of total planting costs, accounting for 75% of the total budget for all pest management efforts (Jaffé 1986; Vilela 1986).

Even though *A. sexdens* is widely distributed, its density decreases in Paraguay, and the species is almost non-existent in Argentina where *Ac. lobicornis* is known to be the major pest in agriculture and forestry (Pilati et al. 1997; de Coll 2003). *Acromyrmex lobicornis* defoliation rates are in the range of 2.5–8.5 kg colony⁻¹year⁻¹, higher than any other *Acromyrmex* species (Pilati et al. 1997). Various *Acromyrmex* species, but especially *Ac. landolti*, are responsible for damage to diverse agricultural crops (mainly grasses and forest trees) in Uruguay (Zolessi and Philippi 1998).

In Costa Rica, Moulart et al. (2002) established that the primary cause of mortality of two indigenous timber species, namely *Vochysia guatemalensis* Donn. Sm. and *Hyeronima alchorneoides* Allemão, was the attack of *A. cephalotes* during the establishment phase. Land holders involved in a Panamanian programme with native species identified *Atta* sp. as one of the most frequent problems in reforestation areas (Garen et al. 2009). They also noted that plantations of Bitter Cedar (*Cedrela odorata* L.) were prone to infestation by LC ants (*Atta* spp.) and the shoot borer, *Hypsipyla grandella* (Zeller), which slowed their growth or dried them up.

4.2.6. Silvopastoral systems and cattle pastures

In Latin America, several LC ant species have been recorded as attacking silvopastoral systems (Ramírez and Calle 2003). In Colombia, intensive *Leucaena leucocephala* (Lam.) de Wit grazing systems are heavily attacked and limited by LC ants during the establishment phase. However, the economic impact is negligible once the system becomes well established (Giraldo 2007). Serrano et al. (1993) found that *Ac. landolti* and *A. laevigata* are the most important grass-cutters in northern South America. However, because small colonies of the latter species grow more rapidly and exhibit high preference for grasses, they are more difficult to control and thus cause greater economic damage to grass cultivars. *Acromyrmex landolti* may be responsible for productivity losses of up to 98% in cattle pastures in the Caquetá region in eastern Colombia (Serrano et al. 1993) and, as in Paraguay, it seems that the presence of LC ants in pasture lands affects the activity of the herds and reduces the economic value of the lands (Fowler and Saes 1986). Robinson (1979) estimated overall annual losses in Paraguay to be between US \$ 6.3–7.9 million (ca. US \$ 20.4–25.9 million at today's value).

4.3. Crop diversification and the attacks of leaf-cutting ants

LC ants attack shade trees in both cocoa and coffee plantations. It can be inferred that if leaf-cutters have a low diversity of plants from which to choose on plantations, their herbivory will be concentrated on the

crop resources. Blanton and Ewel (1985) suggested that a protective effect may be reached if coffee plantations are managed as diversified crops, where the ant exhibits switching behaviour, concentrating on alternative resources when the favoured resource (i.e. coffee leaves) is less abundant. Testing this hypothesis, Varón (2006) found that Costa Rican *A. cephalotes* populations had a higher density in coffee monocultures (without shade trees) than in diversified and tree-shaded coffee plantations. Furthermore, coffee represented 40% of the tissue harvested by LC ants in monocultures but only 10% on diversified farms (Varón 2006; Varón et al. 2007). The same trend was found in cassava in Costa Rica. Blanton and Ewel (1985) reported that a higher vegetation diversity was associated with a reduced total consumption of cassava (leaf area plot⁻¹) by *A. cephalotes*. Furthermore, herbivory by *A. cephalotes* proved to be 10 times higher in Costa Rican cassava monocultures as compared to three complex successional ecosystems (Blanton and Ewel 1985). One explanation for this difference is that the ants (apparently) prefer cassava to other plants and the reduced density of cassava in the diversified systems reduced overall foraging by the ants.

It seems that LC ants prefer shorter plants than taller ones (Vasconcelos 1997). Working in an abandoned successional farm in Brazil, Vasconcelos (1997) found that variations in *A. laevigata*'s diet followed the abundance of the plant *Casearia grandiflora* Cambess., which was preferred by this ant. Also, one attack did not prevent a particular plant from being attacked again, that is, there is no evidence of plant resistance ("memory defence") to LC ant attack. Notwithstanding these findings, Lapointe et al. (1996) claimed that accessions of *Brachiaria* (Trin.) Griseb. grass displayed several characteristics compatible with resistance to *A. landolti*, a specialized grass-cutter in northern South America.

4.4. Leaf-cutting ants as urban pests

For the first time in history, more than half of the world's human population lives in urban areas (DiChristina 2011). New problems associated with urbanization include the emergence of urban pests [*sensu* the World Health Organization definition (Bonney et al. 2008): urban pests are those species implicated in the transfer of diseases, habitat damage or human welfare deterioration with continuous presence and population sizes above (considered) normal levels]. The expansion of agriculture in tropical regions has been associated with a rapid population increase of leaf-cutting ants in clearings (Blanton and Ewel 1985). Several studies have recorded higher LC ant population densities in "man-simplified" habitats than in "natural" ones (Lofgren and Vander Meer 1986). Given that neotropical cities always have trees in places such as streets, gardens, green areas such as

parks, and living fences, it is reasonable that certain LC ant species thrive in such situations. However, the impact of LC ants in urban areas has been insufficiently assessed.

Atta cephalotes is widely distributed in Colombia, covering almost the entire country. This species has invaded natural forests, open and urban areas from sea level to 3500 m.a.s.l. (Mackay and Mackay 1986; Ortiz and Guzmán 2007). Records of the presence of LC ants in Colombian rural and urban areas, especially Cali, are available. In urban habitats, LC ants concentrate wherever non-monocot angiosperms occur (greenhouses, parks, tree hedges, lawns), covering more than 1,200,000 m² of urban lands. Very often, aggregated *A. cephalotes* colonies located in creeks or river banks, weakening the civil engineering structures constructed to hold the river beds. Also, LC ants are responsible for soil subsidence, generating accidents and damaging buildings. Presumably this is a consequence of urban development and/or climate change. These ants appear to take advantage of human environments modified through gardening, urban constructions and the absence of their natural enemies. In these habitats, ants display a high degree of polyphagy, enhanced by their intrinsic capacity to attack both native and introduced plant species used for ornamental purposes. In addition, under these conditions, *A. cephalotes* colonies exhibit rapid and successful dynamic cycles, demanding more food and nesting resources, and they appear to have the physiological and behavioural capacity to withstand control methods. In Colombia as well as in other Latin American countries, the indiscriminate use of toxic insecticides to control ants is a dogmatic approach which may be exacerbating the problem. In the year 2010, building owners in Cali used an average of 2 kg month⁻¹ house⁻¹ chlorpyrifos (approximately 24 kg 1000 m⁻² year⁻¹). An urban area with 200 homes would be using approximately 4.8 tonnes year⁻¹ of this insecticide to control LC ants. The figure is alarming when considering that this product has a broad-spectrum potential and residuality, and contaminates soil and water. It also poses a risk to human and animal health.

In northern Patagonia, *Ac. lobicornis* has expanded its geographic range following existing roads. Nest density along road verges is approximately 10 times higher than in the undisturbed steppe far away from roads (Farji-Brener and Ghermandi 2000). Overall, the environmental changes associated with human expansion appear to promote the proliferation of LC ants in several regions.

The current challenge to researchers is to understand the biological responses of LC ant forest species to the distinct yet simultaneously occurring anthropogenic stresses, and to discriminate among the responses to human intervention, climatic changes and episodic events at various spatial and temporal scales.

5. Control of leaf-cutting ants: current and future measures

Leaf-cutting ants are considered to be difficult to control because they possess both physical and behavioural mechanisms (Dowd 1992; Santos et al. 2006; Giraldo-Echeverri 2009) that allow them to withstand the action of all chemical, biological, mechanical and cultural methods that have been used to date (Boaretto and Forti 1997). So far, with the exception of chemical control, none of the strategies has produced effective results. Most of the effective insecticides have been banned because of their wide, non-selective toxicity. Therefore, alternative methods of control are urgently sought.

5.1. Biological control of leaf-cutting ants

In nature, parasitoids, predators (both vertebrates and invertebrates) and microorganisms together appear to constrain populations of LC ant queens, especially during the nest founding process. Wild and domestic birds, mainly insectivorous and omnivorous species, are important as natural enemies (Boaretto and Forti 1997). Fierro-Calderón (2010) recorded *Theristicus caudatus* (Boddaert), a bird that originates from southwestern Colombia, feeding mainly on LC ant queens. This species together with *Bubulcus ibis* (Linnaeus), *Crotophaga ani* (Linnaeus), and *Vanellus chilensis* (Molina) have been identified as the main predators of winged ants during LC ant nuptial flights (Molina et al. 2010). Mites, ants and beetles are the major arthropod predators of LC ants (Boaretto and Forti 1997). As it was stated above, the scarab *C. virens* decapitates *A. laevigata* queens, using the corpses as an oviposition substrate (Hertel and Colli 1998).

Phorid flies are the most renowned parasitoids of LC ants. A great variety species are present in tropical areas. Phorids are found on plant and flowers nearby the ant nests, attempting to lay eggs on the ant workers' bodies (Orr 1992). If the fly accomplishes this task, the larvae hatches and consumes the ant worker's internal tissues, which eventually kills the parasitized ant (Holldobler and Wilson 2011). The foraging activity of *Atta cephalotes* in Costa Rica (Orr 1992) and *A. sexdens* in Brazil (Bragança et al. 2008) is altered by the presence of the phorid *Neodohniphora* sp.. The increased density of *A. cephalotes* colonies at forest edges compared with the forest interior in Coimbra (Brazil) was explained by Almeida et al. (2008) as a top-down effect resulting from the reduced parasitism by phorids such as *Myrmosicarius* sp., *Neodohniphora arcuata* (Brown), *N. Attae* (Disney), *N. dissita* (Brown), and *N. prolixa* (Brown). In Mexico, Quiroz (in Boaretto and Forti 1997) identified *Megaselia scalaris* (Loew) and *Puliciphora* sp. attacking queens of *A. mexican*. Similarly, in Panama, Feener and Moss (1990) found parasitism of *Apocephalus attophilus* (Borgmeier) on *A. colombica* foragers. More recently, in Argentina,

Elizalde and Folgarait (2010) reported 15 phorid species associated with *Atta* and *Acromyrmex*.

In recent years researchers have been concerned with improving knowledge of the biology of natural enemies of LC ants in order to mass-rear such beneficials in the laboratory, for subsequent release. However, insufficient progress has been made in control programmes. Guillade and Folgarait (2011) provide information on the length of the life-cycles of *Apocephalus setitarsus* (Brown), *Myrmomicarius brandaoi* (Disney), *M. gonzalezae* (Disney), and *Eibesfeldtphora trilobata* (Disney) that might be useful in designing rearing protocols for these parasitoids. That study also recorded a temporal pattern in the relative intensity of parasitism by four phorid fly species reared from *A. vollenweideri* ants collected in Santa Fe, Argentina.

Undoubtedly, the most investigated and widely used biological control options are the use of either entomopathogenic microorganisms (mainly fungi) or plant extracts, summarized in Tables 2 and 3, respectively. An innovative approach is the mix of plant extracts with toxic pathogens as baits, and targeting the ants and the symbiont fungus simultaneously (Table 4). This causes toxicity to workers or to the symbiotic fungus, or to both, with lower environmental impact than chemical insecticides (Almeida et al. 2007). Although the method has shown interesting and promising results, further research is required to improve the attractiveness of the baits.

Throughout the distribution range of LC ants, different fungi (*M. anisopliae* and *B. bassiana*, *Aspergillus parasiticus* Speare, *M. anisopliae* var. *anisopliae*) have been reported to have activity against the ants or as antagonists of the ants' fungal symbiont (*Trichoderma* spp.) (Alves and Sosa Gomez 1983; Carrión et al. 1996; López et al. 1999; Verma et al. 2007). However, despite the promising results of microbial control of LC ants in the laboratory, some obstacles must be overcome. One of these is the gap between the high efficiency rates obtained in the laboratory and the discrete results observed under field conditions (Boaretto and Forti 1997). Basically, there is no concordance between the high control efficiency of the microbial agents tested in the laboratory and their variable and irregular efficiency under field conditions. This mismatch probably reflects the difficulty in assessing and ensuring the chemical and biological stability of the product (Varón 2006; Herrera 2009). However, the most important limitation of biological control is the remarkable ability of LC ants to detect, defend themselves against, and recover from pathogens under natural conditions (Table 4).

The high level of vitality of the ant nest depends on the hygienic conditions of the fungal gardens. *Atta* spp. possess a complex combined morphological caste and behavioural caste (polyethism) system which is tightly linked to the maintenance of the homeostasis inside

their colonies (Wilson 1953; Wirth et al. 2003; Giraldo-Echeverri 2009; Griffiths and Hughes 2010). For this reason, it has been suggested that the workers combine special behavioural and morphological specializations to eliminate antifungal substances and pathogens with potential to harm the colony (Schultz 1999; Currie and Stuart 2001; Mueller et al. 2001; Fernandez 2003; Poulsen et al. 2003; Little et al. 2006). In particular, it has been suggested that the secretion of antibiotic compounds (acids, alcohols, lactones) produced by a pair of exocrine metapleural glands has complex and specialized functions to protect the colony (Holldobler and Wilson 1990; Ortius-Lechner et al. 2000; Mueller et al. 2001; Richard and Mora 2005; Armitage et al. 2011). In addition, it has been shown that the infrabuccal pocket is a complex device that filters particles through the cavity. Fragments of food (plant material, wood, bodies), microorganisms and compounds that pose a potential risk are stored in the form of "pellets" or small balls in the cavity, and expelled from the colony (Mueller et al. 2001). This mechanism has been observed in some Attini, including *A. colombica* (Currie and Stuart 2001) and *Trachymyrmex* cf. *zeteki* Weber (Little et al. 2006). In addition to all specialized defence mechanisms of the ants, the symbiont fungus also has the ability to detoxify toxic compounds (Dowd 1992). Hence, the challenge is to introduce microorganisms and opportunistic generalists into the colony that, under certain circumstances, can alter the growth and development of the symbiont fungus (Rodrigues 2004).

Recent studies have revealed the existence of other organisms involved in the mutualistic association between LC ants and fungi. These microorganisms are either vertically transmitted via the founding queen (Currie et al. 1999) or, eventually, acquired from the surrounding environment (Mueller et al. 2008). They are permanent inhabitants of the colony and appear to protect ants but also the fungus garden against pathogen attacks (Fisher et al. 1996; Carreiro et al. 1997; Currie 2001; Currie et al. 2003; Pagnocca et al. 2008; Haeder et al. 2009; Giraldo-Echeverri 2009; Armitage et al. 2011). One of the best documented aspects is the isolation of *Streptomyces* from the body of *Ac. octospinosus* workers. This produces a potent antifungal to combat the specialized mycoparasite *Escovopsis* that attacks Attini gardens (Currie et al. 1999, 2003; Poulsen et al. 2003; Haeder et al. 2009). Santos et al. (2004) also studied *Burkholderia*, a bacterium that secretes potent antifungal agents capable of inhibiting the germination of conidia in the entomopathogenic *B. bassiana*, *M. anisopliae* and the saprophytic and pathogenic *Lecanicillium lecanii* (Zimm.) Zare & W. Gams and *E. weberi* without affecting the symbiont, *L. gongylophorus*, in *A. sexdens rubropilosa* nests. More recently, Giraldo-Echeverri (2009) found *Serratia marcescens* Bizio associated with the worker caste of *A. cephalotes* and suggested that

Table 3. Plant extracts evaluated for the control of *Atta* and *Acromyrmex* spp.

Target ant species	Plant species	Active substance	Results	References
<i>A. cephalotes</i> and <i>L. gongylophorus</i>	<i>Hymenaea coubaril</i> L. (Caesalpinaceae), <i>Melampodium divaricatum</i> (L.C. Rich) DC (Asteraceae) and <i>Vismia baccifera</i> (L) Triana & Planch (Clusiaceae) (extracts)	Terpenoids (caryophyllene, caryophyllene epoxide, kolavenol and nerolidol)	Laboratory bioassays: with the exception of kolavenol, all compounds displayed deleterious effects upon both ants and fungus	Howard et al. (1988)
<i>A. cephalotes</i>	<i>Tithonia diversifolia</i> (Asteraceae) (whole plant)	None indicated	Field assays showed that green manure of <i>T. diversifolia</i> protects against LC ant herbivory	Giraldo-Echeverri (2005)
<i>A. cephalotes</i> and <i>L. gongylophorus</i>	<i>Canavalia ensiformis</i> L. (Fabaceae) and <i>T. diversifolia</i> (Asteraceae) (leaves)	Attributed to terpenoids and alkaloids	Laboratory bioassays with fresh and dry mulch revealed adverse effects on both LC ant workers and symbiotic fungi	Aubad-López (2011); Valderrama-Eslava et al. (2009); Rodriguez et al. (2008)
<i>A. cephalotes</i>	<i>T. diversifolia</i> (Asteraceae) (leaves and flowers)	Attributed to terpenoids and alkaloids	Laboratory bioassays using dry and fresh extracts of leaves showed toxic effects on LC ant workers	Castaña (2009)
<i>Atta</i> spp.	<i>Canavalia ensiformis</i> (Fabaceae) (leaves)	Attributed to possible fungicide activity of demethylhomopterocarpin	Cessation of ant activity in the field for up to five years	Mullenax (1979)
<i>L. gongylophorus</i>	<i>C. ensiformis</i> (Fabaceae) (leaves)	Active compounds unknown	Reduction of fungal garden volume and possible negative physiological effect on ants	Hebling et al. (2000a)
<i>A. sexdens</i>	<i>Ipomoea batatas</i> (L.) Lam. (Convolvulaceae) (leaves)	Active compounds unknown	Laboratory bioassays. Toxic to ant workers with an inhibitory effect on symbiotic fungus growth	Hebling et al. (2000b)
<i>A. sexdens rubropilosa</i>	<i>Cedrela fissilis</i> Vell. (Meliaceae)	Roots, stems, branches, fruits and leaves	Toxic extracts for ants and symbiotic fungi	Bueno et al. (2005)
<i>A. sexdens rubropilosa</i>	<i>Cipadessa fruticosa</i> (Bl. Bujdr) (Meliaceae) (fruits, branches and leaves)	Mexicanolide limonoids	Toxic to workers and inhibits growth of the symbiotic fungus	Leite et al. (2005)
<i>A. sexdens rubropilosa</i> and <i>L. gongylophorus</i>	<i>Ricinus communis</i> L. (Euphorbiaceae) (leave extracts)	Synergistic activity of fatty acids. Fungicidal activity of ricinine	In laboratory bioassays simultaneous toxic effect on both ants and the symbiotic fungus	Bigi et al. (2004)
<i>L. gongylophorus</i> and <i>A. s.rubropilosa</i>	<i>Sesamum indicum</i> L. (Pedaliaceae) (fractions and subfractions from leaves)	Possibly due to sesamine and a mix of fatty acids. Lignan	In laboratory bioassay, inhibition of symbiotic fungus growth	Bueno et al. (2004); Ribeiro et al. (1998); Bueno et al. (1995)
<i>A. sexdens rubropilosa</i> and <i>L. gongylophorus</i>	<i>Virola sebifera</i> L., <i>Virola</i> sp. (Myristicaceae)	Leaf lignans. Epigalgravin	In-vitro inhibition of symbiotic fungus growth. Activity against ants	Pagnozza et al. (1996)
<i>A. sexdens</i> and <i>L. gongylophorus</i>	<i>Otoba parvifolia</i> (Markgr) AH Gentry (Myristicaceae)	Fruit lignans. Epigalgravin Possibly sesamine	In laboratory bioassays the three compounds adversely affect the ant and fungus symbiont simultaneously	Almeida et al. (2007)
<i>A. sexdens</i> and <i>L. gongylophorus</i>	<i>Helictia puberula</i> RE Fr (Rutaceae) (leaves extracts)	Alkaloids: dictamine, anthranilic acid, kokusagine		

(continued)

Table 3. (Continued).

Target ant species	Plant species	Active substance	Results	References
<i>A. mexicana</i>	<i>Cucurbita maxima</i> Dutch (Cucurbitaceae) (seeds) <i>Azadirachta indica</i> A. Juss (Meliaceae)(seeds) <i>Phyllanthus acuminatus</i> Vahl (Phyllanthaceae) and the Asteraceae, <i>Tithonia diversifolia</i> and <i>Clibadium asperum</i> DC (baits with powdered leaves) <i>Glireschia sepium</i> (Jacq.) Walp (Fabaceae) leaves <i>Azadirachta</i> (Meliaceae) cake	Sesquiterpen farnesol	Temporary repellent	Palacios and Gladstone (2003) Bigi et al. (2004)
<i>A. colombica</i> and <i>A. cephalotes</i>		Not discussed	Short term (7–8 weeks) reduction of the workers activity	Escobar et al. (2002)
<i>Atta</i> spp.		Not studied	In citrus plantations short-lasting reduction in ant activity. Needs to be applied with other practices. Not economical	Gruber and Valdivia (2003)
<i>Ac. lundii</i> Güerin	<i>Ricinus communis</i> (Euphorbiaceae) and the Meliaceae, <i>Melia azedarach</i> L. and <i>Trichillia glauca</i> Oerst ex Planch	Not studied	Laboratory assays using a colony of the species. <i>R. communis</i> had a deterrent effect while <i>T. glauca</i> is toxic by ingestion	Caffarini et al. (2008)
<i>Ac. octospinosus</i>	<i>Mammea americana</i> L. (Calophyllaceae) seeds, <i>Nerium oleander</i> L. (Apocynaceae), <i>Nicotiana tabacum</i> L. (Solanaceae)	For <i>N. oleander</i> , cardenolides such as kaneroside, neridiginoside, neritaloside, neriumoside, nerizoside and odoroside, for <i>N. tabacum</i> , nicotine	<i>Mammea americana</i> seed extract was active by contact, highly insecticidal by ingestion and repellent. The decoction of fresh leaves and the dried leaf juice of <i>Nerium oleander</i> were insecticidal by ingestion and quite repellent. The <i>Nicotiana tabacum</i> leaf extract was highly insecticidal by contact and ingestion, and was very repellent	Boulogne et al. (2012)

the bacterium might confer protection to the colony against the attack of fungal pathogens. Van Borm et al. (2002) documented the diversity of microorganisms that can be found within the bodies of workers of the LC ant *Ac. octospinosus*.

Recently, Folgarait et al. (2011), in an *in vitro* evaluation, found that three *Escovopsis* strains overgrew the *Leucoagaricus* cultivar maintained by *Ac. lundii*, and therefore have the potential to become important biocontrol agents. However, in their assay, the entomopathogenic fungus *Lecanicillium lecanii* seemed to compete *in vitro* with *Escovopsis*. Therefore, current laboratory evidence indicates that the simultaneous use of both fungi for biological control of *A. lundii* would be inadequate.

5.2. Chemical control of leaf-cutting ants

In agroecosystems where LC ant populations are enhanced by habitat simplification, most farmers advocate the use of chemical insecticides as the only method for controlling the ants (Cherrett 1986; Lemus et al. 2008), and they apply these compounds in different formulations: powders, granular and liquid baits, and nebulizers (Boaretto and Forti 1997). The active ingredients of the earlier powder formulations were chlorides, mainly aldrin and heptachlor,

which are now banned in many countries. Phosphate, carbamate and pyrethroid-based products have been extensively used to control LC ants in all neotropical areas (Boaretto and Forti 1997). Mirex (also known as dodecachlor, dechlorane or ferriamicide) was used for several decades (ATSDR 1995; RAPAL 2011) until it was identified as a persistent organic pollutant (UNEP 2011) and was banned in the USA, Argentina, Brazil, Costa Rica, Ecuador, Mexico, Peru and Uruguay (RAPAL 2011). Many commercial products have been scientifically tested for mode of application, dosage and effectiveness against LC ant species. The most relevant studies are summarized in Table 5.

Insufflation has been the most conventional method for applying chemical insecticides, and manual insufflators are extensively used to control small- to medium-sized nests. However, thermal foggers allow the entry of the chemical into all compartments of the LC ant colonies by heating diesel or mineral oil (Boaretto and Forti 1997) and are more efficient for larger nests (> 10 m²). Both systems have been tested with chlorinated products (heptachlor), carbamates (isoprocarb), pyrethroids (deltamethrin, resmethrin, decamethrin), phosphorates (chlorpyrifos) (Boaretto and Forti 1997) and cypermethrin (Escobar et al. 2002). Often, chemical insecticides are also essential

Table 4. Mixtures of entomopathogenic (E) and antagonistic (A) fungi with plant extracts evaluated for *Atta* and *Acromyrmex* spp. control.

Target species	Plant extract	Pathogen	Type of assay	References
<i>Acromyrmex crassispinus</i> Forel, <i>Ac. heyeri</i> Forel and <i>Ac. striatus</i> .	<i>Havenia dulcis</i> Thumb (Rhamnaceae) and <i>Aleurites fordii</i> Hemsl. (Euphorbiaceae)	<i>Beauveria bassiana</i> (E)	Field colonies	Specht et al. (1994)
<i>Atta cephalotes</i>	<i>Hura crepitans</i> L. (Euphorbiaceae) and <i>Canavalia ensiformis</i>	<i>Paecilomyces</i> sp. (E) and <i>Metarrhizium anisopliae</i> (E)	Field colonies	Varón (2006)
<i>Atta</i> spp.	<i>Azadirachta indica</i>	<i>Trichoderma</i> (A) and mounds (A)	Field colonies	Herrera (2009)

Table 5. Chemical products tested for *Atta* and *Acromyrmex* spp. control

LC ant species	Products	Remarks	References
<i>Acromyrmex lobicornis</i> , <i>Acromyrmex heyeri</i> , <i>Acromyrmex striatus</i>	Malathion, parathion, fenthion, trichlorfon, bendiocarb	Ant colonies are inactive after 10 days of the application. Unquantified effectiveness	Juruena (1984)
<i>Acromyrmex subterraneus brunneus</i>	Fenthion, deltamethrin and fenitrothion	90–100% effectiveness	Delabie (1989)
<i>Atta sexdens sexdens</i>	Deltamethrin	50–70% effectiveness	Boaretto and Forti (1997)
<i>Atta sexdens rubropilosa</i>	Fenthion, imidacloprid, beta-cyfluthrin, chlorpyrifos, deltamethrin, acephate and diazinon	100% effectiveness	
<i>Acromyrmex crassispinus</i>	Fenthion, imidacloprid, beta-cyfluthrin, chlorpyrifos, deltamethrin, acephate and diazinon	Fenthion, chlorpyrifos and diazinon were effective in the control of large nests	Link et al. (2000)
<i>Acromyrmex heyeri</i>	Acephate, chlorpyrifos and fenthion	Deltamethrin and acephate were useful and effective in controlling small nests, while chlorpyrifos and fenthion, controlled large nests	Link et al. (2001)

components in granular bait recipes. Baits are carried and introduced in colonies by the ants themselves (Boaretto and Forti 1997). Almost all products have been tried as baits (Boaretto and Forti 1997). Currently, sulfuramid is the main compound used in the control of LC ants in forest plantations in Brazil and Argentina. Granular baits containing fipronile, chlorpyrifos, aldrin (Escobar et al. 2002; Herrera 2009) and diflubenzuron (Boaretto and Forti 1997) are also commercially available.

Because most chemicals have deterrent effects on the LC ants, several investigations have been carried out seeking to increase bait attractiveness, especially using plant extracts. Given that LC ants prefer citrus trees, citrus extracts have proved to be effective in increasing bait attractiveness and as a result are the most commonly used (Herrera 2009). Sorghum, soybean, eucalyptus leaf and cassava flour baits are also available (Boaretto and Forti 1997), as well as products based on wheat flour, cane sugar (Boaretto and Forti 1997; Lima et al. 2003) and blades of jaragua grass *Hypparhenia rufa* (Nees.) Stapf (Poaceae) (Lima et al. 2003).

Many products used as active ingredients for controlling LC ants have been classified as persistent organic pollutants (FAO 2011) and their use has been banned or restricted. Since 2005, the Forest Stewardship Council (FSC) began reviewing its policy on the management and certification of plantations and expressed its concern about the use of highly hazardous pesticides (FSC 2011). Since then, the FSC has promoted integrated pest management and the long-term monitoring of impacts on health and the environment. As a consequence, the FSC has restricted the use of products such as deltamethrin, fenitrothion, fipronil and sulfluramid for controlling LC cutter ants (*Atta* and *Acromyrmex*) (Isenring and Neumeister 2010). This situation represents a serious problem for forestry companies that rely on chemical insecticides for herbivory control because they have been left without an effective alternative control for LC ants. For this reason, many private companies have requested the FSC to postpone the restriction on some chemicals, arguing that few management alternatives are available. In the meantime, companies will promote research directed to designing effective control strategies having less of an environmental impact.

5.3. Mechanical control

Removal of queen ants and compost treatments are simple mechanical control methods. The first method takes into account the timing of the nuptial flight, which has a distinct seasonality, specific to each region. It consists of digging the newly formed mounds (15–20 cm deep) to remove the queen ant, thereby preventing the growth of the colony (Giraldo 2007). This method is commonly used at the small scale,

where there is easy access, such as rural farms, houses and urban parks, and where permanent monitoring is possible. The compost treatment is based on a mixture of organic (leaf litter, poultry manure, molasses, yeasts) with inorganic (agricultural lime and water) ingredients combined on top of the nests. For this, the soil is mechanically removed, using a long, sharpened shovel. Next, the organic materials are evenly spread on the nest, and left covered with a black plastic sheet for two weeks. Armbrecht and co-workers (unpublished study) found that the efficiency of this method was comparable to that obtained using compost incorporated into the soil to control nests of *A. cephalotes*. Results showed significant stress in ant colonies treated by both composted and mechanical mixing with respect to the untreated controls due to the disruption of foraging trails, mound openings, and chamber tunnels. Mechanical removal and compost treatments should be envisaged and promoted as sustainable and ecologically sound management practices across the board: although both methods are effective, economical and environmentally safe, their use should be restricted to small colonies less than four months old.

5.4. Physical control

The use of physical disturbance of the nests (Montoya-Correa et al. 2007) or barriers that preclude the access of foragers to nutrient resources represents an easy and inexpensive way to protect plants grown on a small scale and in urban gardens. It is possible to use clay pots, plastic or rubber water-containing oil or other fluids to prevent the passage of ants. The use of wool, sticky paste and grease for bearings, temporarily prevents ant foraging on plants. Moreover, the refuse dumps of LC ants also act as a short-term barrier against the attack of other ants (Farji-Brener and Sasal 2003; Ballari and Farji-Brener 2006). Although not very practical, refuse dumps around seedlings can be used to delay the attack of some LC ant species for several weeks. In this way the small scale approach may be employed as a short-term, cheap and human-safe method to protect plants. The most important implication of these findings, however, is that the repellent nature of the compounds found in the mounds might be harnessed and lead to alternative, clean methods of ant control (Zeh et al. 1999).

5.5. Cultural control

The diversification of crop systems and rational use of chemicals (pesticides and fertilizers) are the main strategies of cultural control. In Colombia, *Tithonia diversifolia* nurse shrubs interplanted in *Montanoa quadrangularis* tree plantations have reduced the frequency and severity of *A. cephalotes* attack

(Giraldo-Echeverri 2005). *Tithonia diversifolia* also promoted a reduction in the use of chemical fertilizer in silvopastoral systems. This practice reduces fodder attractiveness and prevents biomass loss. It has also been suggested that the incorporation of native trees in pastures and hedgerows enhances biological control in livestock systems. Thus, increasing the diversity of plants favours the establishment of beneficial fauna, especially birds, contributing to the natural suppression of leaf cutter ants (Giraldo 2007; Molina et al. 2010).

The avoidance, by ants, of substances that affect fungal growth might explain the deterrent effects of *T. diversifolia* and other plants on ant foraging behaviour. Laboratory studies have shown that LC ants such as *Ac. ambiguus* learn to avoid plants that contain chemicals harmful to the fungus (Saverschek and Roces 2011).

5.6. Traditional practices

Folk practices such as the use of queens as food by local people (DNP 2010) have not been scientifically evaluated, but they are likely to exert some form of population pressure on the target species. In the department of Santander, Colombia, for instance, people collect the queen ants during the nuptial flight season to consume directly or for use in cooking (DNP 2010). These traditional practices should be promoted. On the other hand, there are very risky cultural practices such as using fire, blowing up colony mounds with gasoline (Escobar et al. 2002; Sunjian and Hongmei, 2006) or introducing animal corpses into the colonies. These traditions are neither practicable or safe, and although still used in rural areas, they should be discouraged.

6. Concluding remarks

Atta and *Acromyrmex* ants are of paramount importance in neotropical ecosystems. They are the main herbivores and soil modifiers but, at the same time, the major pests in cultivated fields along their geographic distribution. Although the various LC species have similar life-history traits, the control of some of them represents a serious and defiant challenge. Given the highly complex ecology of LC ants, a simple and unique control of their herbivory should not be expected. Sound LC ant control strategies must combine and alternate different methods both spatially and temporally. Available scientific information is extensive and profound, although rather redundant. Efforts should be made to synthesize the overall knowledge regarding ecological and socioeconomic aspects of LC ants in order to better understand these complex organisms. A further step should be directed to ecologically sound control programmes tempered to the geographic areas.

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