Ant biodiversity and its relationship to ecosystem functioning: a review

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Ants are important components of ecosystems not only because they constitute a great part of the animal biomass but also because they act as ecosystem engineers. Ant biodiversity is incredibly high and these organisms are highly responsive to human impact, which obviously reduces its richness. However, it is not clear how such disturbance damages the maintenance of ant services to the ecosystem. Ants are important in below ground processes through the alteration of the physical and chemical environment and through their effects on plants, microorganisms, and other soil organisms. This review summarizes the information available on ant biodiversity patterns, how it can be quantified, and how biodiversity is affected by human impacts such as land use change, pollution, invasions, and climate change. The role of ants in ecosystems is discussed, mainly from the perspective of the effects of ground-dwelling ants on soil processes and function, emphasizing their role as ecosystem engineers. Some lines of research are suggested after demonstrating the gaps in our current information on ant-soil interactions.

Keywords: ants; biodiversity; ecosystem engineers; mounds; soil function.

Introduction

"There are more species of ants in a square kilometer of Brazilian forest than all the species of primates in the world, more workers in a single colony of driver ants than all the lions and elephants in Africa" (Wilson, 1975). "Ants are everywhere, but occasionally noticed. They run much of the terrestrial world as the premier soil turners, channelers of energy, dominatrices of the insect fauna… One third of the entire animal biomass of the Amazonia terra firme rain forest is composed of ants and termites, with each hectare of soil containing in excess of 8 million ants and 1 million termites." (Hölldobler and Wilson, 1990).

Although these quotes highlight the importance of ants in terms of biodiversity (number and abundance of species) and their roles in ecosystems, it is surprising to realize that ants are not included in this respect in ecological (Pianka, 1988; Ricklefs, 1990) or conservation-related (Dasmann, 1984; Meffe *et al*., 1997) textbooks, and are hardly mentioned in soil ecology textbooks (Killham, 1994). Fortunately, as further studies are generated and more integrative approaches are used, this pattern is slowly changing thanks to the knowledge generated by soil ecologists (Paton *et al*., 1995; Lavelle and Spain, in press).

This paper reviews, as exhaustively as possible, what is known about the biodiversity of ants and their roles in ecosystem functioning. In particular, it refers to ground ants and

soil functioning. Firstly, it introduces what is known about ant biodiversity and how it can be quantified. Secondly, it addresses how human impact affects ant biodiversity highlighting the role of ants as indicators of change. Thirdly, it reviews the ways in which ants influence soil functioning, putting greater emphasis on ants as ecosystem engineers. Finally, through identifying information that is still lacking, it indicates ways in which knowledge can be generated to fill the gaps about the role of ants in soil functioning.

Ant Biodiversity

Ants are classified in a single family, the Formicidae, within the order Hymenoptera, and are social insects which have been evolving successfully since the Cretaceous. The known living ants involve 16 subfamilies, 296 genera and 15 000 species, around 10 000 of which are described (Bolton, 1994). However, the number of species still remaining to be discovered and described is incredibly high (Holldobler and Wilson, 1990). Imperfect classification of some groups (specially due to the presence of sibling species) complicates biodiversity assessments even further. The geographical regions with greatest number of genera decrease in the following order: IndoAustralian, Neotropical, Oriental, Australian, African, Palearctic, Nearctic, and Malaysian, among which the Neotropical and African areas have the greatest number of endemic genera, and the Nearctic and Oriental the least (Bolton, 1994). Table 1 gives an indication of ant species biodiversity throughout the world.

Ants can be found in any type of habitat from the Arctic Circle to the Equator (Brian, 1978), although they are absent from Iceland, Greenland and Antarctica (Hölldobler and Wilson, 1990) and some islands lack native ants (Wilson and Taylor, 1967). The number of species declines with increasing latitudes, altitudes, and aridity (Kusnezov, 1957; Fowler and Claver, 1991; Farji Brener and Ruggiero, 1994; Samson *et al.*, 1997). Despite the fact that tropical areas and continental forests are amongst the poorest known, these areas have the greatest recorded species diversity (Hölldobler and Wilson, 1990). Using comparable sampling methods, the non-canopy ant community found in $4 km^2$ of forest lead to 98 species in Brazilian Amazonas, 66 in southern Brazil, 41 in Australia, and 12 in Tasmania, which represents a gradient from tropical and sub-tropical to temperate forests

Table 1. Ant richness* in different regions of the world

Region	Number of species
West Indies, Mexico, Central and South America	2233
North America, North of Mexico	585
USA	400
Europe	429
Africa (sub-saharan)	2500
Asia (parts of this region)	2080
New Guinea, New Britian and New ireland	275
Australia	1100
New Zealand	23
Polynesia	42

*From Holldobler and Wilson (1991) and Groombridge (1992).

(Majer and Delabie, 1994). Landscape heterogeneity promoted by river disturbances and by orogenic effects also seems to be correlated with the biodiversity of ants that presumably associate in mutualistic relationships with plants (Davidson and McKey, 1993; Folgarait, 1996).

The local diversity of ants is also very high. A survey of $250 \, km^2$ of a Malaysian rain forest yielded 460 species (Majer and Delabie, 1994). In $2.6 \, km^2$ of lowland rainforest in New Guinea 172 species were found (59 genera; Wilson, 1959), while 219 species (63 genera) and 272 species (71 genera) were recorded in $1.6 \, km^2$ of forest and cocoa plantation at Ghana (Room, 1971) and Brazil, respectively (Kempf, 1964). The temperate ant fauna is also impressive, in $5.6 \, km^2$ in Michigan, 87 species (23 genera) were found (Talbot, 1975), and in $8 \, km^2$ in Florida 76 species (30 genera) were recorded (van Pelt, 1956). Even relatively arid zones can have high levels of ant species richness; for example in $18 \, km^2$ of semi-arid south Australia, 248 species (32 genera) were collected (Andersen and Clay, 1996). Flooding reduces soil ant biodiversity as shown for an Amazonian rain forest where species richness decreased from 98 in the uplands, 88 in the lowlands to 55 in the flooded areas (Majer and Delabie, 1994).

Methods of estimating ant biodiversity

Ants, in general, are very easy to sample. Baiting techniques, pitfall traps, aspirators, litter sifting, Berlese-Tullgren or Winkler funnels for litter or soil core samples, and hand collections with forceps or nets are among the most common methods to sample ground foraging ants. All these methods are easy to use, cheap, and not incredibly time consuming. It should not take more than three days of full-time work using several methods to obtain a complete list of the ant fauna from 1 ha of soil (Hölldobler and Wilson, 1990). However, exhaustive inventories on broad geographical scales are probably impossible. A comparison of the litter and soil ant fauna have shown that a combination of pitfalls, litter sifting, baiting and hand sorting increase the efficiency of species captures in comparison to any single method by itself (Majer and Delabie, 1994). The addition of ground baiting and Winkler analysis for litter samples increased the efficiency of richness estimations by 20–30% when compared to the combined use of pitfalls, hand collections, and sweep net (Majer, 1996). In communities dominated by one or few species that monopolize food resources, ground baiting alone might give misleading results on biodiversity. Folgarait *et al.* (1997a) have shown that only the abundant *Camponotus punctulatus* appeared at four different types of baits while 10 ant species were recorded simultaneously in pitfalls at the same sown tropical pasture. Andersen and Patel (1994) found similar results with the dominant meat ant, *Iridomyrmex purpureus*, in Australia. Although pitfall traps represent the most common method use to sample ants, it may not capture the whole and diversity if the traps are not left for long in the field, if the number of traps is insufficient, if the size is not adequate, if other ants except the surface-active ones are to be quantified, or if the habitat is not very open (Majer, 1997). In fact numerous studies have pointed out the need to use more than one method in quantifying ant biodiversity (Romero and Jaffe, 1989; Olson, 1991; Majer, 1997).

Cross-site or ecosystem-site comparisons can be made standardizing sampling efforts and calculating similar biodiversity indexes, or species-accumulation or rarefaction curves. Estimations of biodiversity by fitting different data distributions are much more feasible to obtain if presence/absence data is used. It is also much easier to estimate the richness of

species assemblages locally than to measure the complementarity (distinctness or dissimilarity) of local inventories. Alternatively, ratios between known values of species richness to estimate unknown values, represent a different strategy for measuring biodiversity for poorly known taxonomic groups or localities (assuming that the relevant ratios are constant among the entities compared) (Colwell and Coddington, 1994). The next two long-term, large-scale examples give an idea of what is known about assessing ant biodiversity.

Ants, beetles and spiders were sampled from four forest types, over three seasons, using two collecting methods in Australian hardwood forests (Oliver and Beattie, 1996). Specimens were sorted by non-specialists to morphospecies and later by specialist taxonomists. Species accumulation curves flattened only for ants showing that this sampling effort was enough just for this group. No significant correlations were found between these groups implying that there are no surrogate (indicator) species to estimate alpha diversity. However, there was a negative correlation between ant and beetle diversity. Assessment of turnover (beta diversity) showed that ants and beetles exhibited different assemblages in different forests, ants being more speciose at dry sites and beetles at wet ones, but with similar turnover. As ants were found easier and faster to identify by parataxonomists, these social insects could be used as a surrogate group for beta diversity estimations. The summer and spring pitfall trap samples were most representative of alpha and beta diversity in comparison to the more intensive sampling. The results were similar whether ant species or morphospecies were used.

The biodiversity assessment used in La Selva Arthropod's project ("ALAS" in Costa Rica's OTS Biological Station) corresponds to a quantitatively structured inventory stratified by habitat, time and space, and using three methods of capture: Berlese, Malaise and Fogging (the last two to capture mainly arboreal ants, although Malaise traps may capture rare species that live elsewhere). Longino and Colwell (1997) found that after a year of intensive sampling (twice per month or bimonthly in 16 sites of the tropical forest) they had captured 253 of the 400 species of ants known in the area, and based on projections of accumulated curves found that new methods (litter sifting to find cryptic litter-inhabiting species, manual collection or visual observation to capture army ants, specialized plant-ants, and tramp species) should be used to efficiently capture additional species. The greatest diversity in sampling was obtained by a combination of two methods; however, Malaise and fogging were found to be redundant. Interestingly, they found temporal, spatial or habitat stratification did not increase the efficiency of their inventories (specially for Berlese extractions which deal with ground ants).

Changes in ant biodiversity

Land use

In general it has been shown that agricultural practices such as heavy grazing, irrigation, drainage, fertilization, mowing, conventional tillage, ploughing, and reseeding, reduce ant biodiversity and/or biomass, and colony densities (Kanowski, 1956; Breymeier, 1971; Galle, 1972; Williard, 1973; Pisarski, 1978; Diaz, 1991; Perfecto and Snelling, 1995; Radford *et al.*, 1995; Table 2). Despite this reduction in biodiversity, ants seem to tolerate, recover, or re-invade the same areas after disturbance (Table 2). Perfecto and Snelling (1995) showed that the ant ground community is likely to suffer more reductions in biodiversity than those of the arboreal strata in coffee bushes as technological intensification increases in coffee plantations. In a few cases, however, ant abundance actually

Table 2. Ant biodiversity under different types of human-made disturbances and in comparison to control sites

Habitat and Location	Richness and (abundance) in the natural environment	Type of disturbance	Richness after disturbance	Abundance after disturbance	Reference
Meadows, Polonia	4 spp (1.5–1.6 nests/m^2, 162 ind/m^2)	1) short-term fertilization 2) fertilized for 25 years	1) decrease, 3 spp 2) 2 spp, only dominants	1) variable: 1.3–1.6 nests/m^2, 112–187 ind/m^2 2) decrease: 0.75 nests/m^2, 136 ind/m^2	Petal 1976
Meadows on peat soils, Polonia	3 spp (0.03–0.24 nests/m^2)	drainage of peats at different times and sites	increase, 4–6 spp, only if lands drained >25 years ago	decrease in nest density (0.008–0.040, except lands drained 100 years ago); no change in colony size	Petal 1991
Open and closed scrub heath, Australia	35 spp	farm paddock	decrease, 12 spp	disappear subordinate and cryptic species, increase generalized myrmicines and climate specialists	Keals and Majer 1991
1) Heath, 2) Wandoo woodland, Australia	1) 65 spp (1.9 ind/pitfall/d) 2) 89 spp (1.9 ind/pitfall/d)	farmland	1) decrease, 32 spp 2) decrease, 29 spp	1) increase, 5.1 ind/pitfall/d 2) increase, 5.5 ind/pitfall/d increase opportunists and generalized myrmicines, ant nest density similar	Lobry de Bruyn 1993
Eucalypt dominated tropical savanna, Australia	22–27 spp (7–9 ind/pitfall/d)	1) burned annually 2) burned every two years	1) increase, 38–42 spp 2) increase, 38–49 spp both change the dominant functional groups	1) increase, 15–20 ind/pitfall/d 2) variable 8.8–19.3 ind/pitfall/d	Andersen 1991
Eucalypt dominated woodland, Australia	20 spp (9.3 ind/pitfall/d)	1) burnt 2) grazed	1) similar, 19 spp 2) decrease, 16 spp	1) increase, 13.6 ind/pitfall/d 2) increase, 15.3 ind/pitfall/d	Andersen and McKaige 1987
Primary lowland rain-forest, Costa Rica	69–87 spp	successional sites after clearing	decrease, 42–61 spp		Olson 1991
Sclerophylllus fynbos, South Africa	14 spp (7.2 ind/pitfall/d)	1) different times since burnt 2) pine plantation	1) increase, 20–29 spp 2) decrease, 9 spp	1) increase, 12.2–47.0 ind/pitfall/d, greater equitativity 2) decrease, 1.5 ind/pitfall/d, less equitativity	Donnelly and Giliomee 1985

Table 2. (*Continued*)

Habitat and Location	Richness and (abundance) in the natural environment	Type of disturbance	Richness after disturbance	Abundance after disturbance	Reference
Natural sub-tropical grasslands, Argentina	7–10 spp (0.9–1.6 ind/ pitfall/d)	7 years old pastures of different spp	decrease, 5–8 spp (but not per pitfall)	increase in abundance of 1 species, 0.8–3.4 ind/pitfall/d	Folgarait *et al.* 1997a, in rev.
Lowland tropical forest, Costa Rica	37–43 spp	1) abandoned cacao 2) productive cacao 3) productive banana	1) similar, 36 spp 2) decrease, 16–26 spp 3) decrease, 13–14 spp	1) similar abundance 2 and 3) greater dominance of few groups, lower equitativity	Roth *et al.* 1994
Secondary tropical forest, Cote d'Ivoire	(100.8 ind/m^2)	rubber plantations of different ages		decrease, 24–28 ind/m^2 except in the 5 year old one	Gilot *et al.* 1995
Inundated rainforest, Amazonia	1) dry season (2762 ind/m^2) 2) rainy season (1116 ind/m^2)	mixed crop plantation		1) decrease, 134 ind/m^2 2) decrease, 520 ind/m^2	Adis and Albuquerque 1989
Peruvian rainforest, Amazonia	(555 ind/m^2)	1) secondary forest 2) different crops 3) different pastures		1) decrease, 290 ind/m^2 2) decrease, 272–370 ind/m^2, except in traditional systems 3) decrease, 68–256 ind/m^2, except in traditional systems	Lavelle and Pashanasi 1989
Protected savanna, Colombia	(472 ind/m^2) [in gallery forest, 862 ind/m^2]	1) burned and grazed savanna 2) sown pastures 3) crops		1) decrease, 331 ind/m^2, except at low stocking rate 2) variable, 75–534 ind/m^2, 3) decrease, 11–19 ind/m^2	Decaens *et al.* 1994
Dry sclerophyll jarrah, Australia	19 spp (21.5 ind/pitfall/d)	1) burnt jarrah 2) pine plantation 3) farmland 4) bauxite mined area	1) similar, 20 spp 2) decrease, 10 spp 3) decrease, 4 spp 4) decrease, 6 spp	1) decrease, 16.2 ind/pitfall/d 2) increase, 111.1 ind/pitfall/d 3) decrease, 14.1 ind/pitfall/d 4) decrease, 0.3 ind/pitfall/d 1, 2, and 3 with higher equitativity and 4 with lower	Majer 1977

Location	Species	Mine type	Species response	Abundance response	Reference
Eucalyptus and speargrass-dominated savanna woodland, Australia	33–35 spp	uranium mines with different ages of rehabilitation	reduction greater as less time of rehabilitation (4 spp) and further from undisturbed sites (7 spp)	increase the abundance of dominant species: exotic or aggressive native ones	Andersen 1993
Rainforest, Brazil	55–98 spp (0.7–1.6 ind/ pitfall/day)	bauxite mines rehabilitated with different vegetation	decrease, 54–59 spp	increase the abundance of generalists and specialists decrease, 0.02–6.1 ind/pitfall/d	Majer 1996
Open forest, Queensland	26–30 spp (5–18 ind/pitfall/d)	mineral-sanded mine with different rehabilitation times	decrease, 4–24 spp	increase, 9–19.7 ind/pitfall/d, mainly due to tramp or dominant species	Majer 1985
Hummock grassland, Australia	16–18 spp (13.4 ind/pitfall/d)	1) rehabilitated waste dump 2) recently treated iron ore mine surface	1) similar, 16 spp, but different assemblage of species 2) decrease, 7–11 spp	1) decrease, 9.6 ind/pitfall/d 2) similar, 12.4–13.1 ind/pitfall/d, high dominance of some species	Dunlop and Majer 1985

increased, for example, when low impact land use activities are conducted as occurs in traditional crop and pasture systems (Lavelle and Pashanasi, 1989), or at low cattle stocking rates (Deacens *et al.*, 1994). Along a gradient of increasing grazing intensity in the semi-arid Chaco region in Argentina, overall ant species richness changed little across sites but favoured opportunists and hot climate specialists (over cryptic and specialized predators) at highly disturbed areas (Bestelmeyer and Wiens, 1996). Table 2 illustrates studies in which ant biodiversity has been recorded under different types and extents of land disturbance in comparison to controls. In many cases, despite a reduction in ant species richness, the overall abundance of ants increased due to the dominance of aggressive or exotic species. In all cases where the disturbance was by fire, ant species diversity increased afterwards.

In western Australia, it was shown that road construction produce the greatest long-term reduction in ant species alpha diversity, followed by agricultural clearing, mining, urbanization, and rangeland grazing, although agricultural clearing and rangeland grazing have the greatest difference in comparison to the original diversity which characterizes the land unit (Majer and Beeston, 1996).

Pollution

Ants exhibit a greater resistance to pollutants in comparison to other invertebrates, especially to radioactivity (Torossian and Causse, 1968; Le Masne and Bonavita-Cougourdan, 1972) and to industrial pollutants (Petal *et al.*, 1975), probably due to the fact that: (1) only a ~10% of ants are outside of the nest and then are exposed to these negative effects; and (2) ants can change their patterns of activity to times when exposure to pollutants is less dangerous. However, the density of ant colonies and their sizes decrease with increasing levels of pollution (Petal, 1978a).

Ant species have been used successfully as soil indicators of minesite rehabilitation (Majer, 1983; Majer and de Kock, 1992; Andersen, 1993; Majer, 1996) and its richness has been shown to correlate well with the composition of plant species (Majer *et al.*, 1982) and invertebrate (Andersen, 1997), as well as, with microbial biomass (Andersen and Sparling, 1997). Ants may have positive or negative influences in cases where habitats are rehabilitated by seeding plants depending on their seed preferences or on the presence of elaiosomes (food ant rewards) in the seeds because the ants may act as granivores (negative effect) or dispersers (positive effect) (Majer, 1984).

Global climate change

No specific "climate change" experiments have been conducted to evaluate ant performance. However, correlations between ant distributions, rainfall and temperatures (Farji Brener and Ruggiero, 1994; Andersen, 1995) as well as activity patterns under changing conditions of temperature and humidity (Shumacher and Whitford, 1974; MacKay, 1981; Cerdá *et al.*, 1997), may allow us to predict which species can cope with changes in global temperatures and rainfall. For example, hot climate specialists should be able to tolerate increases in temperature due to the greenhouse effect.

Latitudinal comparisons have shown that ant diversity is positively correlated with temperature and rainfall. If higher temperatures increase the probability of fires or floodings, then the competitive interactions within ant communities might change the rules of coexistence leading to new assemblages affecting biodiversity (Wiens, 1977; Folgarait *et al.*, 1997b). In a restoration study, Andersen (1993) has shown that fire breaks the

dominance of *Acacia* plants and allows a greater diversity of ants as a consequence of increased plant heterogeneity.

Introductions/invasions

Exotic ants have repeatedly been shown to have negative impacts on native ant, invertebrate and vertebrate communities (Williams, 1994, and references therein). Exotic ants have also shown to negatively affect restoration efforts by impeding establishment of native ant communities (Majer, 1985).

Some native ant species can invade new areas and produce a similar negative effect on the native fauna as do exotic species. For example, *Camponotus punculatus* in Argentina invades post-agricultural fields where it becomes dominant, decreasing significantly the abundance of other ant species (Folgarait *et al.*, 1997a). In a native area in Argentina where *Solenopsis richteri* reaches unusually high densities, the ant community is very poor. This successful invasion seems to be due to the low abundance of top-down regulators such as *Solenopsis*-specific parasitoids, and this situation in turn, changes the outcome of competitive interactions among the ant species of the community (Folgarait *et al.*, in prep.). When the abundance of a particular ant species is positively correlated with disturbance, this invasive species can be used as an indicator of disturbance in the area (Andersen and McKaige, 1987).

Functional role of ground ants in ecosystems

Although soil ants may belong to different trophic levels (leaf-cutter and harvester ants as primary consumers; predators and melivores as secondary consumers), probably all can be classified as ecosystem engineers (Jones *et al.*, 1994). This is because of their basically similar effects on soil structure and processes which directly and indirectly affect the flow of energy and material in ecosystems (see below), as well as the habitats of other species (Table 3).

Ants also have an important effect on the ecosystem due to their voracity. Omnivore ant species living in meadows can consume up to 3% of the primary production and 40% of the prey biomass available per season (Petal, 1980). An average-size colony of *Formica polyctena* can consume 6×10^6 insects (259 MJ) and 155 litres of honeydew (686 MJ) from 0.27 ha over the season (Horstman, 1974; cited in Petal, 1978b). Leaf-cutter ants can reduce 17% of the annual leaf production of a tropical forest (Cherret, 1989), and one *Atta* nest can consume 1-2 tons of fresh leaf material per year (Coutinho, 1982).

Many arthropods (myrmecophiles) live in ant mounds as specialized inhabitants of refuse piles, brood or queen chambers, storage areas, or the same bodies of the ants. Ant mounds covered with plants may also allow the development of a rhizosphere-related fauna. Besides the well known basidiomycete fungi cultivated by leaf-cutter ants (Weber, 1972), other microorganisms are also associated with ant nests. Anthills may create patches of mycorrhizal enrichment (Friese and Allen, 1993) which can help the establishment of plants (Allen *et al.*, 1989) due to the dispersion of fungal spores (McIlveen and Cole, 1976). Non-mychorrizal microbes also seem to favour plant productivity in richer anthill soils (McGinley *et al.*, 1994). As ants stimulate the abundance of amonifying bacteria while earthworm casts promote that of actinomycetes, these two groups of ecosystem engineers have different effects on soil processes, although both locally increase the concentrations of nutrients as soil fertility decreases (Petal *et al.*, 1977).

Table 3. Effect of different ant species on anthill soil and anthill soil-related parameters in comparison to adjacent areas outside of the nest influence. I, D, S = refer to increase, decrease or the same value in comparison to the control

Ant species (food habit)	Location	Habitat	Chemical changes			Physical changes	Effect on microbes	Effect on plants	Reference
			chemicals	pH	OM				
Atta colombica (leaf-cutter)	Panama	Rainforest	I = P, K, Ca, Na, S, Cu		I				Haines 1975, 1978
Atta laevigata (leaf-cutter)	Venezuela	Drained savanna with groves	I = N, Ca, Mg S = K, Na, Al, P		I			might favour grove formation	Farji Brener and Silva 1995
Pogonomyrmex occidentalis (seed harvester)	USA	desert watershed 1) grassland, low slope 2) mixed shrubland, edge of lake 3) sub-shrub-grass forb at mid slope	1) I = N; D = Ca, Mg; S = Na, K, P 2) S = for all 3) I = N; D = P; S = Ca, Mg, Na, K, P		S S S			I = % cover by four spring annuals and one annual	Whitford and DiMarco 1995
Pogonomyrmex rugosus (seed harvester)	USA	semiarid mountain pine/juniper forest	I = N, P, K	variable depending on site		S = bulk density Variable soil texture		lower plant richness Variable % plant cover	Carlson and Whitford 1991
Lasius flavus (nectivorous)	England	chalk grassland	I = K, Na, P; D = N; Variable = Mg, Mn, Ca	variable depending on site		I = soil particles <0.5 mm; D = stone % D = bulk density		allows the existence of plants w/high affinity for anthills, mainly winter annuals and few perennials	King 1977 and references therein
Solenopsis invicta (predator)	USA	coastal plain	1) top 5 cm I = P, K, Ca, Mg 2) 15–20 cm I = K S = P, Ca, Mg	S S	I I	1) D = bulk density 2) S = bulk density			Lockaby and Adams 1985

Myrmica sp. (predator)	Poland	fertilized and unfertilized meadows	I = P, C Variable = Ca, Mg, K	S		I	I = fungi; Variable = ammonifying bacteria; D = Actinomycetes	yes (but not specified)	Petal 1980
Lasius niger (omnivore)	Poland	Uncultivated meadows	I = P, K, Na, Mg; D = C; S = Ca	I		D	I = fungi and ammon. bacteria; D = Actinomycetes	invaded first by plant species with rhizomes	Czerwinski *et al.* 1971 Petal *et al.* 1970
Formica canadensis (omnivore)	USA	mountain meadow	I = P,K; D = Fe, Zn, Mn, Cd, Pb; S = N, Ni, Cu	S		D		lower richness, more eveness, non-myrmecochorous species w/high affinity for anthills	Culver and Beattie 1983; Beattie and Culver 1977
Formica fusca (omnivore)	USA	abandoned agricultural field	1) top 20cm: I = Ca, P: D = K; S = Mg; 2) below 20cm: I = K; S = Ca, P, Mg	I; S	I = soil particles <2mm (mainly clay %)	D; S			Levan and Stone 1983
Formica cinerea (omnivore)	USA	praire	I = P, K, N	I	I = clay % D = bulk density				Baxter and Hole 1967
Camponotus punctulatus (omnivore)	Argentina	1) sown pastures 2) abandoned rice fields	1) I = N, K 2) I = N, K, P 1 & 2) S = Ca, Mg, Na	S; S	1 & 2) S = sand, clay and silt%.	I; I		allows the existence of plants w/high affinity for anthills, but similar richness and plant community structure	Folgarait *et al.* 1997c

Soil modification

The construction of ant nests changes the physical and chemical properties of the soil increasing its drainage and aeration through the formation of underground galleries, and transforming organic matter and incorporating nutrients by food storage, aphid (Homoptera) cultivation, and the accumulation of faeces and corpses (Brain, 1978). These bioturbation effects occur in the topsoil as well as in the subsoil whether the ant nest is subterranean or forms a mound. In the case of non-mound nests, the amount of soil translocated within the subsoil and packed into pre-existing chambers could be very high. For example, attine (*Mycocapurus*, non leaf-cutter ants) bioturbation are responsible for the characteristic occurrence of smooth-walled chambers and galleries in andosol soils in Martinique (Eschenbrenner, 1994). Chambers and galleries are lined with fine particles smeared with macerated/regurgitated plant fragments or faecal material. These cavities are infilled with a porous mixture of soil aggregates (750–2000 μm) sometimes mixed with cocoon sacks (Humphreys, 1994).

Two types of mounds which have different pedological impacts can be built by species that construct conspicuous mounds (Paton *et al.*, 1995). Type I mounds are crater-shaped, small in diameter and height, consist of mineral soil piled mainly as sand grains linked by a clay matrix, and are very susceptible to erosion (i.e. *Pogonomyrmex rugosus* or *P. occidentalis* in Table 3). Type II mounds are much larger, have elliptical shapes, persist for much longer, are sometimes covered by vegetation, and are made of reworked soil material. These mounds are often cemented making them very resistant to erosion as in those of *Camponotus punctulatus* (Table 3).

The movement of subterranean soil to the surface through ant activity can be substantial. The highest mounding rates recorded are about $10\,\text{t ha}^{-1}\,\text{y}^{-1}$ from moist subtropical and temperate systems (Paton *et al.*, 1995). The activities of desert ants may also lead to high soil turnover rates such as $420\,\text{kg ha}^{-1}\,\text{y}^{-1}$ in Australia (Briese, 1982) to $842\,\text{kg ha}^{-1}\,\text{y}^{-1}$ in the USA (Whitford *et al.*, 1986). Agricultural settings are no exception. In Argentina, *Camponotus punctulatus* ants move $2100\,\text{kg ha}^{-1}\,\text{y}^{-1}$ of soil in constructing their mounds in sown pastures (Folgarait, unpubl.). From a comparison of global rates of animal turbation, ants scored second ($\sim5000\,\text{g m}^{-2}\,\text{y}^{-1}$), after earthworms ($\sim15000\,\text{g m}^{-2}\,\text{y}^{-1}$) but ants have a wider geographical distribution than the latter (Paton *et al.*, 1995). In fact, it has been proposed that ants are as important as earthworms in soil transformation (Gotwald, 1986). The impact of ants as soil movers is clearly shown by leaf-cutters in the tropics where they are the most important agents of soil modification (Alvarado *et al.*, 1981; Cherret, 1989). For example, a colony of *Atta sexdens* in Brazil was found to deposit on the surface an amount of soil that covered $100\,\text{m}^2$, occupied $23\,\text{m}^3$, and had a weight of 40 tons (Autori, 1947). A chamber of *Atta capiguara* of 1.5 m width and 5 m height was found to contain 500 kg of organic matter in Brazil (Amante, 1964).

Ants have been shown repeatedly (see below) to have an effect on nutrient immobilization and humification (Anderson and Flanagan, 1989; Lavelle *et al.*, 1992). Soil ant refuse piles function as food sources and habitat for the associated fauna, and the speed of mineralization within these garbage sites is increased. This is particularly marked in leaf-cutter ants, as the leaves carried by the ants to the nests are immediately decomposed by the fungus, by-passing the many steps associated with the normal cycling of such leaves in the forest (Lugo *et al.*, 1973). The most important changes in the soil produced by ants can be divided in the following four categories:

Physical changes

Physical changes are related to the soil profile, the organic matter is buried deeper increasing the water-holding capacity, and small particles are taken from deeper layer to the surface (Petal, 1978b; Table 3). Ant bioturbation activity is shown by the presence of channels, chambers, soil aggregates, and maculae in the soil. The last diagnostic features refers to small/elliptical spots of faint colour that contrast to the background colour of the soil (Humphreys, 1994). The network of galleries and chambers increases the porosity of the soil, increasing drainage and soil aeration (Denning *et al.*, 1977; Gotwald, 1986; Majer *et al.*, 1987; Cherrett, 1989) and reducing bulk density (Baxter and Hole, 1967; Rogers, 1972; Table 3). Studies in agricultural fields have shown that the effectiveness of water infiltration depends on the spatial and temporal pattern of ant burrows and whether the biopores remain open under conditions of heavy irrigation (Lobry de Bruyn and Conacher, 1994; Wang *et al.*, 1996). Water infiltration and rainshadow also depend on the amount of vegetation covering the mound and the permeability of the cement used by the ants (mainly in type II mounds).

Sometimes new A horizons are being developed with materials from B horizons (Alvarado *et al.*, 1981), in other cases formation of soil horizons are impeded (Salem and Hole, 1968; Mandel and Sorenson, 1982). Lobry de Bruyn and Conacher (1990) have shown in two types of soil and land use that the particle size distribution of anthill materials were similar to control soils, and that in all eight species studied, ant activity lead to homogenization of the soil texture profile within the anthill. Table 3 does not show a clear pattern of textural changes occurring on the mounds. Paton *et al.* (1995) point out that texture-contrast soils can be produced by bioturbation and rainwash when the material (from bedrock or as a result of epimorphism) is heterogeneous; in contrast when the soil is homogeneous, a change in structure but not texture should be expected as a result of the same processes. Therefore, both texture and structure should be characterized in comparing anthills with topsoil outside the mound influence. The biofabrics present in abandoned nests may last for quite some time (Humphreys, 1994).

Chemical changes

Although some of the chemical changes observed vary with soil characteristics or the species of ant involved (McGinley *et al.*, 1994), in general, most studies have shown an increase in organic matter, P, N, and K in ant mounds in comparison to adjacent soil samples (Salem and Hole, 1968; Czerwinsky *et al.*, 1969; Petal, 1978b; Mandel and Sorenson, 1982; Table 3). These differences seem to be greater in poorer soils (Czerwinsky *et al.*, 1971; Petal, 1992) and appear to depend on ant colony size, biomass and turnover (Petal *et al.*, 1992). The elements showing an enrichment in ant mounds (Table 3) occur as soluble and mobile (K, Na, Ca, Mg) and their mineral stability is greatly affected by biospheric interactions that promote their release by weathering (Paton *et al.*, 1995).

In some cases, the extent of nutrient increase suggests an input from external sources (Levan and Stone, 1983) or the development of new relationships, i.e. presence of VAM or more active decomposition (Folgarait, unpublished). Few studies have found ant activity to influence soil pH (Wiken *et al.*, 1976; Table 3), although there is some evidence that ant activity lowers the pH in alkaline soils and increases it in acid soils (Petal, 1980). Ant mounds have pH values between 5 and 7 (Table 3), and overall ant abundance seems not to be affected by soil pH (Lavelle *et al.*, 1995). pH values may depend also on the amounts

of organic matter available to break down and on the mass of plant roots present on the mound, which both reduce pH values.

Changes in nutrient and energy fluxes

Decomposition processes (mainly first stages of mineralisation) carried out by fungi and amonifying bacteria, are very active and more represented in ant mounds in comparison to adjacent soils. The humification process is delayed due to the decrease of Actinomycetes in ant nests (Czerwinski *et al.*, 1971; Jakubczyk *et al.*, 1972), and the effect of anthills on humus fraction composition seems to be ant-species dependent (Petal and Kusinska, 1994). Nests of *Atta colombica* in Panama increase by 38 times the fluxes of 13 chemical elements in comparison to surrounding areas of forest, probably due to the greater root activity close to the ant nests (Haines, 1978). In Puerto Rico, leaf-cutter ants have been shown to increase net plant productivity in 1.80 kcal m^{-2} probably because their activities increases the availability of phosphorous in the soil (Lugo *et al.*, 1973).

The contributions of ants to nutrient cycling are likely tot be more important in poor than in fertile soils (Petal, 1992). In infertile environments with low organic matter and complex trophic webs, ants speed up the return to the soil of nutrients held in the bodies of animals, while earthworms have a similar effect in fertile soils which are characterized by simple trophic structures (Petal, 1978b; Petal *et al.*, 1977).

The energy flow through ants could be higher than that through the homiotherms living in the same habitat (Golley and Gentry, 1964). For example, the production of ant species for a short-grass plain costs 0.6–6.1 kJ m^{-2} or 0.2–0.3% of the primary production (Petal, 1978b), for a meadow is 24–280 kJ m^{-2} or 0.2–2.8% (Kajak *et al.*, 1971), for a pasture is 3.1–15.1 kJ m^{-2} or 0.01–0.11% (Petal, 1974), and for an old field is 58–75 kJ m^{-2} or 3.2% of the primary production (Wiegert and Evans, 1967).

Vegetation changes

In general, plant species composition and relative abundance differs on the mounds and close to them, in comparison to adjacent areas (Woodell, 1974; Andersen, 1982; Horvitz and Schemske, 1986; Table 3). Ants can disperse plant propagules (Wilson, 1992) and anthills facilitate the appearance of invasive plant species (Bucher, 1982; Folgarait *et al.*, 1996; Farji Brener and Margutti, 1997) and sometimes changes or quickens the course of plant succession (Jonkman, 1978). The effect of anthills on vegetation depends on the age of the mound and seems to persist as long as the colony remains active (Jakubczyk *et al.*, 1972; Folgarait *et al.*, 1997c).

In infertile sites, the enrichment of the soil through the actions of ants is a key element for the development of vegetation (Coutinho, 1984; Sarmiento, 1984; Medina and Silva, 1990). Sown pastures grown on soil from anthills have greater productivity than those growing in non-anthill soil (Folgarait *et al.*, in prep.). This finding highlights the importance of ant activity in agricultural production.

Ants as ecosystem engineers

"Physical ecosystem engineers are organisms that directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials. The ecological effects of engineering on other species occur because the physical state changes directly or indirectly control resources used by these other species." (Jones *et al.*, 1997). From this review, it is clear that ground ants create and modify habitat

for other organisms and modulate the availability of resources by creating the biomantle (i.e. that part of the soil whose properties are a consequence of the long-continued biological activity of soil fauna pedoturbators; Johnson, 1990). In a study designed to quantify the bioturbation effects of the mesofauna at Sydney Basin, Humphreys (1994) has shown that the funnel ant (*Aphaenogaster longiceps*) contributes to more than 80% of the amount of soil moved to the surface by the soil fauna. Surprisingly, ants are hardly mentioned in the literature on ecosystem engineers (but see Jones *et al.*, 1994; Brussaard *et al.*, in press).

Jones *et al.* (1997) argue that the persistence through time of those physical structures that grow and replace themselves, should promote the dependency of other organisms on the autogenic/allogenic resources or habitats created by these structures. Anthills particularly fit this definition and I predict that landscapes with persistent mounds should have greater diversity than those without these engineers. According to Jones *et al.* (1994)'s characterization of ecological engineers, ants should also have high spatial and temporal ecosystem impacts because of the high population density they may attain, the length of time the populations remain at a local site or landscape level, the resistance of the mounds to erosion, the durability of their constructs even after nest abandonment, and because of their effects modulating water flux, soil fabric and texture, nutrient availability for plants, and habitat for other fauna.

Hacker and Gaines (1997) suggest that ecosystem engineers may act as facilitators increasing species diversity, particularly in physically or biotically stressed systems. As mentioned above, ants facilitate the development of other organisms in their mounds, including unique plants that otherwise would not exist (King, 1977; Folgarait *et al.*, 1996), or increase the amounts of some microorganisms (Czerwinski *et al.*, 1971; Petal, 1980). Studies from sites under rehabilitation accord well with this concept as ants seem to be very successful invaders in highly disturbed sites (Majer, 1983, 1992; Andersen, 1990 York 1994), and specially seem to facilitate the development of other species, for example microorganisms, under these situations (Andersen and Sparling, 1997). However, caution should be taken in extrapolating from this idea. For example, if an aggressive ant species re-invades successfully a disturbed system, it may happen that the course of succession of the ant community might stop at low levels of ant species richness or abundance. This seems to be the case in post-agricultural fields in Argentina with *Camponotus punctulatus* ants (Folgarait *et al.*, 1997a), as well as with meat ants in Australia (Andersen and Patel, 1994).

Research needs

There are many questions that still need to be addressed in order to understand the role of ant biodiversity in soil functioning. Most of the data reviewed here come from a few particular systems which were, in most cases, studies with other goals than understanding the roles of ants in soil processes and ecosystem functioning. Very little is known about how human activities affect this group, and even more basic questions still remain unanswered. For example, it is not clear if there are any keystone soil ant species. Is it the same if any ant species disappears in terms of the maintenance of the correct system functioning? Or within which web of interactions are soil ants involved, how sensitive to disturbance is this web and how rapid is recovery following alteration? Or if there is any relationship between the role of ant species and their relative abundance, is the role of ecosystem engineer ant species dependent on their abundances? Only a few aspects of some

of these questions have been touched in studies conducted so far. The following approaches could serve as guidelines in starting to address some of the above issues:

(1) *The removal of ant species* through chemical insecticides with no residual effects. If biodiversity composition and function is measured before and after ants have been excluded, the role of the ''most important'' ant species on ecosystem functioning can be determined. The advantage is that a particular ant species can be deleted and its effect on the ecosystem can be followed; in most cases this removal does not necessarily imply the removal of other organisms simultaneously. If deletion is conducted one species at a time, we can learn which species are keystone or redundant, and if different levels of removal are performed, we can find out if abundance/biomass correlates well with the importance of such species on ecosystem function. The limitations of this method are: (1) time, as it may require a considerable period for the effect to become evident, (2) it requires repeated chemical applications to prevent new colonies from invading the experimental plot; and (3) it might be restricted to obvious nest-builder ants, as litter-cryptic ant species might be impossible to find and remove.

(2) *The addition of known ant species*, by introducing founder queens or implanting new colonies. This has the advantage of biodiversity manipulation, and may be an excellent method to address how invasive a species might be and why some exotic species do much better in some continents or habitats than in others (Folgarait, in prep.). If new colonies are being added, then matched experimental plots, with the simultaneous addition of one ant species (receptor site) and deletion of the same species (donor site), can be followed to determine the success of deletion versus addition experiments in their relative impact with respect to a particular ecosystem process. However, it might take a long time until any effects become apparent.

(3) *The use of disturbed environments*, *or those invaded by exotic/tramp ant species*, where ant biodiversity drops dramatically and the whole community composition changes. These sites should be studied with paired non-disturbed sites (or non-invaded) or habitats with less disturbance to quickly understand the role of ants and which ecosystem processes are affected. (These comparisons may be done under different situations of soil types and disturbance regimes.) In order to take the most advantage from space-for-time substitution studies, the sites should be paired so as to guarantee that the greatest number of other variables are the same. It is also of fundamental importance to monitor plots simultaneously for changes in functions and processes, in addition to measuring changes in ecosystem composition and structure, to find out if the easier-to-measure structural characteristics can be used as surrogates of their function (Lament, 1995).

(4) *The use of environments that have been studied already for other purposes like long-term research sites*. At these sites, a full description of the ant fauna should be carried out to establish functional groups and specific roles for key taxa. Later, information from different groups and abiotic characteristics that are being measured simultaneously should be compared to identify any emerging patterns. These patterns may also allow us to generate specific predictions and design well formulated experiments that can combine an interdisciplinary approach to understand soil functioning.

(5) *Biogeographical studies* can give insight not only into biodiversity structure but also into biodiversity function. If lists of species and some information on ecosystem processes are available throughout a latitudinal gradient, correlative studies might suggest if some species or if the diversity of an ant genus or guild is important for ecosystem functioning.

Conclusion

In comparison to other soil organisms, ants are one of the few groups for which we have accumulated some information in terms of their natural history, and to a less extent, about the ecosystem services they provide. However, the real dimension of their contribution to the latter such as in nutrient cycling, decomposition of organic matter, bioturbation, and in the suppression of soil borne diseases and pests (Brussaard *et al.*, in press) is unknown. There is an urgent need to quantify this contribution as ants are very diverse and abundant, exhibit many types of relationships with other soil biota, and are found in most terrestrial environments of the planet. The direct and indirect contribution of ants to soil health integrity, and the resilience of their response to human disturbance, make ants good candidates to use as soil bioindicators of human impact or restoration success. The information summarized here suggests many patterns about the role of ants in the ecosystem. Researchers should take advantage of this knowledge and should design experiments to relate structural and functional biodiversity and to test how this relationship is affected by human intervention. Mound building ants can also become a model system in which to study how engineers affect soil habitat and resources, locally and at the landscape level.

Acknowledgements

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