Is competition a significant hallmark of ant (Hymenoptera: Formicidae) ecology?

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Abstract

Community ecology has a clear need to develop an understanding of the structure and dynamics of natural communities. Interspecific competition is considered key in structuring local ant communities, and it has been described as the "hallmark of ant ecology". The goal of this literature review is to summarize the evidence supporting the importance of competition in structuring ant communities. First, we describe ant dominance hierarchies, paying special attention to species ranked at the highest level, i.e., dominants. We also establish criteria to standardize the definition of species dominance at both global and local scales, in order to allow comparisons among studies conducted in different regions and at different spatial scales. In particular, we discuss the factors that affect competition, such as trade-offs between dominance and thermal tolerance, as well as between dominance and food discovery, habitat complexity, disturbance, parasitism, and predation. Then, we analyse the relationship between patterns of local and global species richness and the degree of dominance present in communities. Finally, we present the different methodologies, both traditional and modern, used by ant ecologists to test for the effects of competition in ant communities and highlight the advantages and disadvantages of each. The current review supports, to some degree, the reigning paradigm that competition is the predominant structuring force in ant communities. However, it also lays out clear evidence that competition might be less important than has previously been assumed. We suggest that a complex network of interactions involving different abiotic and biotic factors drives the structure of ant communities. We call for more studies to analyse the relative importance of the different factors that structure ant communities, an effort which would improve ant ecological theory.

Key words: Hierarchies, dominant ants, dominance-thermal tolerance trade-off, dominance-discovery trade-off, disturbance, habitat, review.

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Introduction

Community ecology has a clear need to develop an understanding of the structure and dynamics of natural communities. Nevertheless, the complexity of multispecies systems and the various patterns found in different biogeographical areas make this task difficult. Ants are an apt study system for community-level studies because they have highly diverse lifestyles, occur in many different habitats, and are relatively easily sampled. They are also one of the most abundant and influential invertebrate groups in terrestrial ecosystems (WILSON 1990). Ants are important in below- and above-ground processes because they alter the physico-chemical environment of soils and affect plants (e.g., pollination and seed dispersal), microorganisms, and other soil organisms (FOLGARAIT 1998). The 12,649 known species of ants (OHIO STATE UNIVERSITY 2013) are estimated to make up about 10 - 15% of the world's animal biomass (75% of the total insect biomass) (HÖLLDOBLER & WILSON 1990). The ecological dominance of ants, defined as their impact on other species of their community (GREENSLADE 1976, ANDERSEN 1992), is matched by their extraordinary geographic range. Ants are abundant in most of the world's principal terrestrial environments; some species have even adapted to the most stressful or disturbed habitats. Ants share with plants and other sessile organisms the ability to monopolize space and other resources, and therefore influence other species in the areas they occupy (ANDERSEN 1991). This ecological dominance of terrestrial environments has been attributed to the evolution of a highly organized social life, and the existence of multiple lifestyles, ranging from "sessile" herbivores (e.g., leaf-cutting Attini) to highly mobile carnivores (e.g., ecitonine army ants).

Tab. 1: Main characteristics of ant species ranked at different levels in the dominance hierarchy. This hierarchical scheme only applies to ant species that occupy the same guild.

Level of the hierarchy	Colony size (# workers)	Recruitment type	Degree of aggressiveness	Area defended	Example genera
Dominants	$10^4 - 10^7$	Group, Mass	High	Territory	*Iridomyrmex, Formica, Oecophylla, Eciton, Atta*
Subdominants	$10^3 - 10^4$	Tandem, Group, Mass	High	Food	*Camponotus, Lasius, Pheidole, Tetramorium*
Subordinates	$10 - 10^3$	None, Tandem, Group	Low	Nest	*Cataglyphis, Leptothorax, Plagiolepis, Melophorus*

For decades, competition has increasingly become the dominant theme in ant ecology studies. The eusociality and modular nature of ant colonies buffer them against predation and environmental stress (ANDERSEN 1991, DAVIDSON 1998), and many ants behave as generalized scavengers and exudate-feeders (HÖLLDOBLER & WILSON 1990). Thus, competition appears to be ubiquitous in ant communities (DAVIDSON 1998). In recent decades, a large number of studies, both descriptive and experimental, have examined the structure of ant communities and the role of competition therein. Many, perhaps even most, ant species appear to affect one another's abundance, spatial distribution, and behaviour by employing aggressive techniques that range from the use of chemical repellents to the establishment of territories (see review in HÖLLDOBLER & WILSON 1990, ANDERSEN & al. 1991, ANDERSEN & PATEL 1994). Nevertheless, the role of competition in structuring ant communities has been controversial. Evidence for competition has predominantly been based on observations of interference behaviour between foragers or colonies and temporal and / or spatial patterns of species distribution. However, several experimental studies have more directly tested whether or not interspecific competition is instrumental in shaping ant communities (see the section "Testing the effects of competition on ant communities" below for a detailed description of the different methodologies used to do this). Given the features described above (their diverse lifestyles and habitats as well as ease of sampling), ants are a particularly suitable research subject when studying this topic. The objectives of this review are to (1) elucidate the importance of competition in structuring ant communities, (2) identify the factors that mediate the importance of competition, and (3) evaluate the methodological approaches used to test for the effects of competition on ant communities.

Dominance hierarchies

Ant species have been organized into dominance hierarchies based mainly on differences in food collection behaviour and aggressiveness (Tab. 1). These hierarchies are relatively consistent and robust within and across different biogeographic regions, with more highly ranked species largely outcompeting lower ranked ones (e.g., VEPSÄLÄINEN & PISARSKI 1982, MORRISON 1996, CERDÁ & al. 1997). Aggression and avoidance behaviours provide the basis for these dominance ranks; less behaviourally dominate species quickly leave or are driven away upon encountering a more behaviourally dominate species. In the first classification of ant foraging behaviour, WILSON (1971) distinguished three categories of ants: extirpators, opportunists,
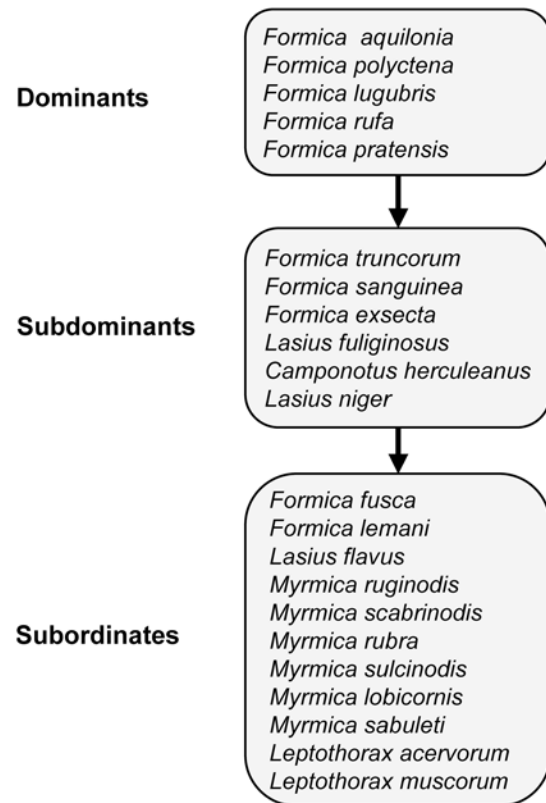

Fig. 1: A three-level competition hierarchy in Finnish taiga ant communities. Modified from SAVOLAINEN & al. (1989).

and insinuators. Extirpators are dominant: They aggressively defend the food resources that they exploit. Opportunists discover food resources quickly and exploit them before other ants arrive. Insinuators arrive in small numbers and discretely steal food from baits occupied by behavioural dominants. However, the three-level competition hierarchies of VEPSÄLÄINEN & PISARSKI (1982) and SAVOLAINEN & al. (1989) provide the most well-defined ecological classification of ant species and are based on both a species' aggressive behaviour and its impact on the other species. They distinguish between dominant (or territorial) species, subdominant (or encounter) species, and non-aggressive (or submissive) subordinate species (Fig. 1). Dominant ants are highly aggressive species that predominate numerically, have mutually exclusive distribution patterns, and occupy large, continuous territories (MAJER & al. 1994). Among dominant ants, there are highly competitive ants, such as species of *Formica, Iridomyrmex* and *Oecophylla* in natural communities, and *Solenopsis* and *Linepithema*
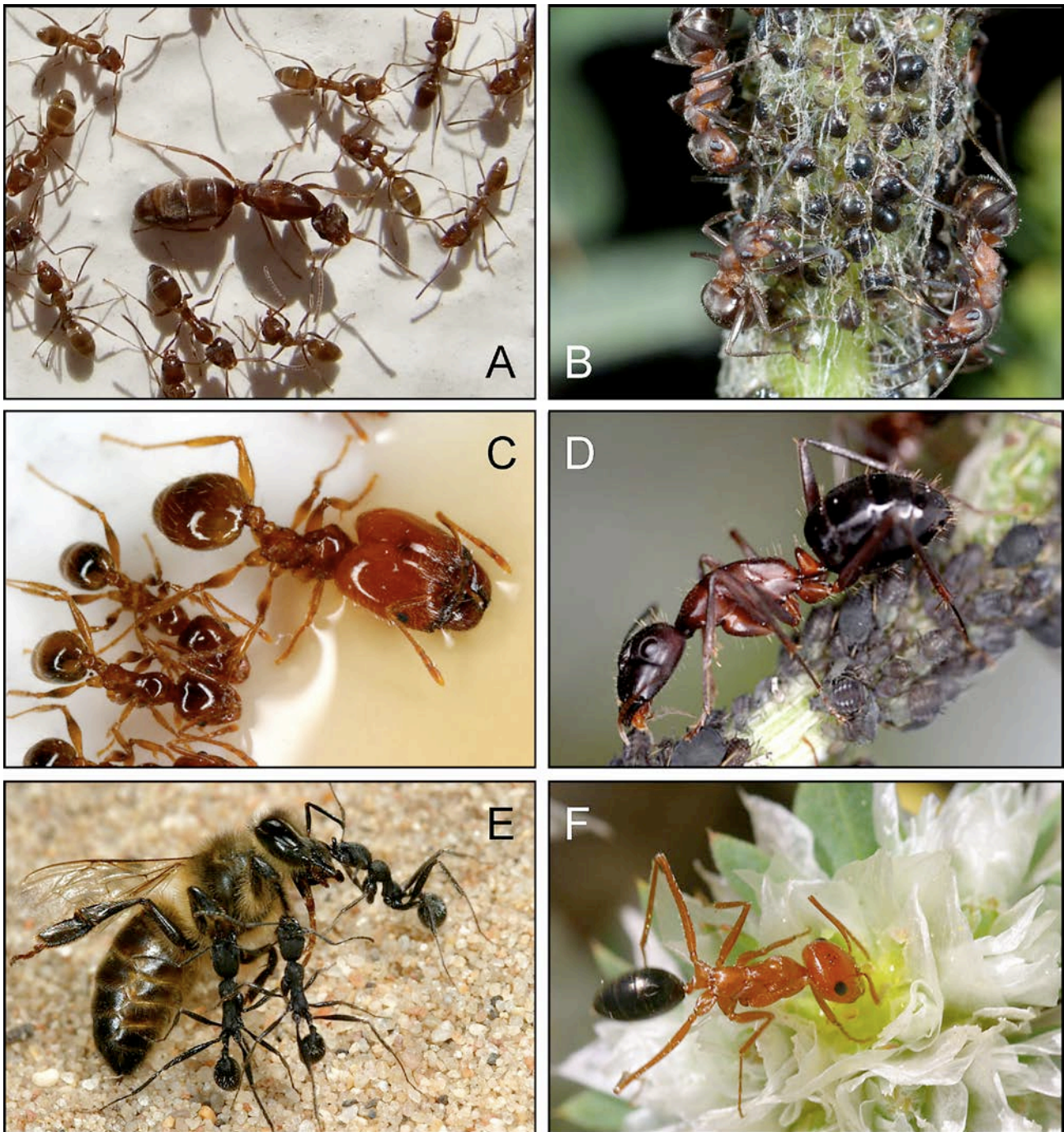
Fig. 2: Photographs of ants of different ranks in the dominance hierarchy in Mediterranean communities. Two dominant species are pictured in: A) queen and workers of the Argentine ant, *Linepithema humile*, a dominant invasive species (photo credit: Elena Angulo) and B) workers of *Formica lugubris*, a dominant and territorial species from the Pyrenees Mountains, collecting honeydew from Homoptera (photo credit: Lluís Comas). Two subdominant species are pictured in: C) soldier and minor workers of *Pheidole pallidula* at a bait (photo credit: Fernando Amor) and D) a worker of *Camponotus sylvaticus* collecting aphid honeydew (photo credit: Fernando Amor). Two subordinate species are pictured in: E) workers of *Aphaenogaster senilis* cooperatively carrying a dead honeybee (photo credit: Fernando Amor) and F) forager of the thermophilic *Cataglyphis rosenhaueri* collecting nectar from a *Paronychia argentea* flower (photo credit: Fernando Amor).

humile in disturbed communities (Fig. 2). Subdominant species are non-territorial, but aggressive when defending or trying to take over concentrated food resources (Fig. 2). They are capable of reaching moderate densities in areas where dominants are absent or in lacunae in a mosaic of dominants (MAJER & al. 1994, SAVOLAINEN & al. 1989, ARNAN & al. 2011). Subordinate species have small colonies, simple or non-existent recruitment systems, and they avoid physical contact with workers of other colonies and species, except when their own nest is attacked (Fig. 2).

On the definition of species dominance in ant communities

It is very difficult to give only one definition of dominance. This key concept has been widely used in ant ecology with very different meanings. Here we only aim to show the main differences between the most frequent definitions. An important caveat: These definitions arise from a competition framework and are relative to ants occupying the same guild.

Behavioural dominance

This type of dominance specifically refers to the relative access to food resources that species have as a consequence of their behavioural interactions (CERDÁ & al. 1997). A behaviourally dominant species is one that is capable of exerting a strong influence on other species: It initiates attacks, and its presence elicits avoidance behaviour on the part of others (e.g., ANDERSEN 1992, CERDÁ & al. 1997). However, behavioural dominance does not necessarily have an effect on ant abundance or competition: WITTMAN & GOTELLI (2011) studied the eight most common ant species in the Siskiyou Mountains and found that pairwise behavioural data did not predict species co-occurrence.

Ecological dominance

This type of dominance takes into account a given species' impact on others. A species is ecologically dominant if it occurs at a large proportion of food resources, monopolizes most of them, and has far greater representation at food resources than would be expected from its presence in the area (ANDERSEN 1992, CERDÁ & al. 1997). DAVIDSON (1998) considers ecological dominance to be a combination of behavioural and numerical dominance.

According to ANDERSEN (1992), **numerical dominance** refers only to the abundance of a species whereas **functional dominance** indicates the strength of its competitive influence on other species (it is equivalent to ecological dominance). See PARR & GIBB (2009: Box 5.1, pp. 83 - 84) for details on the calculation of different dominance scores.

Aggressive, dominant species use interference to exclude other ants from food resources (FELLERS 1987, SAVOLAINEN & VEPSÄLÄINEN 1988, PISARSKI & VEPSÄLÄINEN 1989, CERDÁ & al. 1998a). According to this definition, any species that is abundant and wins competitive interactions with other species might be considered dominant. Thus, functionally or ecologically dominant ants can be from both dominant and subdominant levels within the dominance hierarchy (ANDERSEN 1995). However, given their high abundance, activity, and aggressiveness, and because they monopolize large territories, only the dominant (= territorial) species of the dominance hierarchy are considered as dominant in a global context (SAVOLAINEN & VEPSÄLÄINEN 1988, ANDERSEN 1992, ARNAN & al. 2011). They have been widely studied and have obtained much attention.

A variety of taxa – belonging to completely different taxonomic (and also ecological) groups – have been described as dominant (HÖLLDOBLER & WILSON 1990). In Australia, the behaviourally dominant taxa that reach their maximum abundance in hot and open environments are exclusively members of the subfamily Dolichoderinae (ANDERSEN 1995, GIBB & HOCHULI 2004), although other taxa

(e.g., *Oecophylla smaragdina*) can play the same role in forested areas (ANDERSEN & al. 2007, ARNAN & al. 2011). In cold-temperate forests, the dominant species of the genus *Formica* (especially *rufa* and *exsecta* groups) are the major structuring forces of ant species assemblages (SAVOLAINEN & VEPSÄLÄINEN 1988, DESLIPPE & SAVOLAINEN 1995, ANDERSEN 1997). However, it is worth noting that these dominant species are not very widespread around the world (ANDERSEN 1997; Tab. S1, Appendix, as digital supplementary material to this article, at the journal's web pages). In most ant assemblages worldwide, subdominant species largely act as dominants and have a strong competitive impact on the remainder of the local community (CERDÁ & al. 1997, PARR 2008). In communities lacking territorial species, hierarchical relations are much less predictable (DOBRZANSKI & DOBRZANSKA 1975), and subdominant, non-territorial species are shifted upwards in the hierarchy (SAVOLAINEN & VEPSÄLÄINEN 1988, SAVOLAINEN & al. 1989, ARNAN & al. 2011). These other species, albeit less aggressive and abundant, might also play an important role in structuring communities through competition (e.g., CERDÁ & al. 1997, RETANA & CERDÁ 2000, PARR 2008, STRINGER & al. 2007).

In short, the term "dominant species" has historically been inconsistently used, at least in ant community ecology. Species abundance and interactions at baits have generally been used to assess relative behavioural dominance (e.g., FELLERS 1987, ANDERSEN 1992, 1995, 1997, CERDÁ & al. 1997, RETANA & CERDÁ 2000, LEBRUN 2005, PARR & al. 2005, ARNAN & al. 2012). Based on these criteria, many species might be considered dominant, including both dominants and subdominants of a theoretical dominance hierarchy (see Tab. 1). In any case, those species ranked as dominant in different studies might ecologically behave very differently and, consequently, their competitive impact on the whole community might also be different (see FEENER & al. (2008)'s illustration that hierarchies are context-dependent and that the same species may rank differently in different places). Therefore, it is important to establish in advance, as well as clarify, the criteria for considering a species dominant. If we wish to obtain global patterns beyond the large inconsistencies currently observed among worldwide ant communities, we must use uniform definitions so we can properly compare the results of different studies (at both local and regional scales).

Factors affecting competition

In a recent work, FEENER & al. (2008) made a pertinent observation about competition in ant communities: "In the absence of any compensatory mechanisms, the inevitable outcome of linear dominance hierarchies is competitive exclusion of all but the most dominant species, but single-species ant communities are typically rare in nature." In the next sections, we will review some of these compensatory mechanisms (ecological trade-offs) and other factors (such as habitat complexity, disturbance, or predation) that may act on ant community organization by modifying the expected competitive outcome.

The trade-off between dominance and thermal tolerance

The foraging activity of ants and other small invertebrates is particularly sensitive to abiotic fluctuations in the physical environment, mainly temperature, but also moisture,

light, and wind (see CROS & al. 1997, and references therein). Among these, temperature is considered to be the primary physical factor affecting ant foraging and metabolic rate (but we cannot ignore that humidity is frequently correlated with temperature). Most ant species forage when temperatures are between 10°C and 45°C (HÖLLDOBLER & WILSON 1990). Temperatures outside this range may be considered stressful because they are often near or surpass the critical thermal limits of many ant species (BESTELMEYER 1997, CERDÁ & al. 1998a, BERMAN & al. 2010).

Nevertheless, some ant species have evolved extreme thermal tolerances; they are active either during very high or very low temperatures. Thermophily refers to the ability to be active even when temperatures approach lethality, the hottest moments in an already hot environment (for ants, when temperatures are higher than 45°C, HÖLLDOBLER & WILSON 1990). Thermophilic ant species forage at the highest occurring temperatures, which are close or equal to the ants' thermal limits (WEHNER & al. 1992, CERDÁ & al. 1998a). At the opposite end, cryophily is less well documented in ants (but see KIPYATKOV 2006, MAISOV & al. 2007, BERMAN & al. 2010). Cryophilic species operate near the lower range of environmental temperatures (TALBOT 1943, HÖLLDOBLER & TAYLOR 1983, HEATWOLE & MUIR 1989, BESTELMEYER 1997): They start foraging at just above freezing and cease when the temperature reaches about 20°C. There is a rough correlation between thermal tolerance and the environment in which species occur, with desert species being most tolerant of high temperatures and some (but not all) cold-temperate forest species best tolerating low temperatures (HÖLLDOBLER & WILSON 1990). Nevertheless, there are large differences in preferred foraging temperatures among the species of the same community (HEATWOLE & MUIR 1989, CERDÁ & al. 1998a, LESSARD & al. 2009a, WITTMAN & al. 2010, WIESCHER & al. 2012). These preferences result in large temporal variability in foraging rhythms among sympatric ant species (LYNCH & al. 1988, MARSH 1988, FELLERS 1989, CROS & al. 1997). Nevertheless, STUBLE & al. (in press), in a deciduous forest ant assemblage in North America, observed temporal niche segregation between dominant and subdominant species. However, they found no evidence of a temperature-based niche partitioning.

In boreal and tropical areas, dominant and non-dominant species forage at similar temperatures (SAVOLAINEN & VEPSÄLÄINEN 1988, ANDERSEN 1992). Nevertheless, in more environmentally stressful habitats from other areas of the world, dominant ants are largely restricted by environmental conditions, whereas subordinates are active over a wider (or different) range of temperatures (FELLERS 1989, BESTELMEYER 1997, CERDÁ & al. 1997, 1998a, LESSARD & al. 2009a, WIESCHER & al. 2012). Such is the case in open Mediterranean areas and deserts. In these structurally simplified habitats, daily fluctuations of ground temperature are very high and maximum midday temperature may reach over 50°C in the summer (CROS & al. 1997). Although low temperature has been considered the principal abiotic stress influencing ant community structure (ANDERSEN 1995), extremely high temperature is also an important stress for ants, and largely determines competitive dynamics within some communities (CERDÁ & al. 1997, 1998a). In such communities, the dominant species in the competitive hierarchy are heat-intolerant, probably because
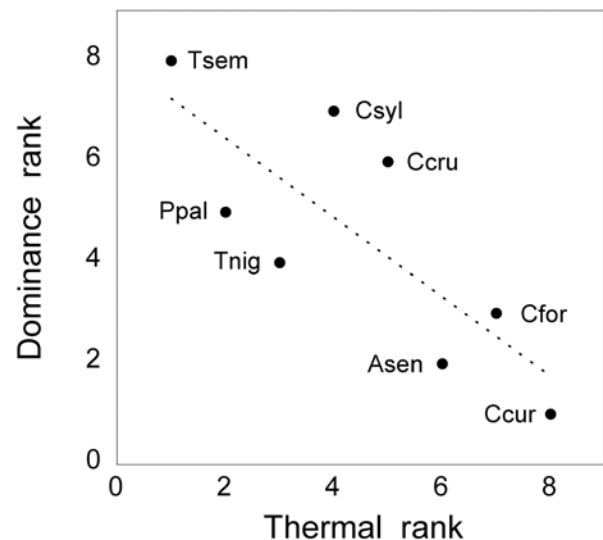

Fig. 3: Trade-off between thermal tolerance and dominance of scavenger ant species from an open Mediterranean grassland (Canet de Mar, Barcelona, NE Spain). Species are ranked from highest (8) to lowest (1) dominance (based on their aggressiveness at baits) and from highest to lowest thermal preference (according to the maximum temperature at which they are active). Abbreviations: Tsem – *Tetramorium semilaeve*; Csyl – *Camponotus sylvaticus*; Ccru – *Camponotus cruentatus*; Ppal – *Pheidole pallidula*; Tnig – *Tapinoma nigerrimum*; Cfor – *Camponotus foreli*; Asen – *Aphaenogaster senilis*; Ccur – *Cataglyphis cursor*. Data from CERDÁ & al. (1998a).

high temperatures cause the rapid chemical decay of pheromone trails (VAN OUDENHOVE & al. 2011, 2012), making it harder for ants to follow them. These species always operate within the lower range of environmental temperatures, whereas many subordinates are heat-tolerant and forage at the highest occurring temperatures (CERDÁ & al. 1997, 1998a). The activity curves of dominants and subordinates show little overlap, because the latter are active during the day, whereas the former are more active during the afternoon and night (HEATWOLE & MUIR 1989, CROS & al. 1997).

These differences in temperature preference between dominants and subordinates have led researchers to propose an inverse relationship between dominance and adaptation to physical stress (FELLERS 1989, CROS & al. 1997). The dominance-thermal tolerance trade-off is expected to apply only if temperatures show large differences between day and night (which mainly occur in open habitats such as grasslands or shrublands, but much less frequently in woodlands). An example of this trade-off between dominance and thermal tolerance is shown in Figure 3: When the eight scavenger ant species of a Spanish Mediterranean grassland (data from CERDÁ & al. 1998a) are ranked from highest to lowest for dominance (according to the hierarchy established from aggressive encounters at baits) and thermal preference (according to the maximum temperature at which they actively forage), we obtain a negative relationship. The species that dominate (in spite of technically being sub-dominants) baits in this community forage at lower temperatures than subordinates (CERDÁ & al. 1998a). The

existence of such thermal niches within the ant community might limit interspecific interactions and permit more effective partitioning of available food resources (HEATWOLE & HARRINGTON 1989, CERDÁ & al. 1998a, b, c). In the Siskiyou Mountains (USA), in habitats with pronounced daily temperature variation, ant community organization and foraging abundance at the local scale appear to be primarily controlled by thermal tolerance, and only secondarily by biotic interactions (WITTMAN & al. 2010). LESSARD & al. (2009a) have suggested that another dominance-thermal tolerance trade-off exists in ant assemblages in the southern Appalachians (USA); behaviourally dominant species forage at warmer temperatures, whereas subordinate species forage at a wider range of temperatures, including colder ones. LESSARD & al. (2009a) have proposed two alternative explanations for these differences in the thermal niche: (1) Dominants always forage at or near their optimal temperatures (described as risk-free temperatures in CERDÁ & al.1998a) because of intrinsic metabolic limitations; and (2) subordinates are competitively excluded from their optimal range and thus forced to forage at suboptimal (colder) temperatures to attain resources. *Prenolepis imparis*, a dominant species, forages at high temperatures in the summer, but also forages during the coolest months of the year, which suggests that competitive exclusion might account for the observed patterns (LESSARD & al. 2009a). Even if ant species are organized in linear dominance hierarchies, the dominance-thermal tolerance trade-off may not operate in all habitats, as observed in some Florida (USA) ant communities (WIESCHER & al. 2011). Shrub habitats are thermally stressful, and subordinates found in them forage at higher temperatures, thus exhibiting greater thermal tolerance than dominant species. On the contrary, in thermally moderate forest habitats, there is scant evidence for the dominance-thermal tolerance trade-off, implying that other processes control species coexistence. SANTINI & al. (2007) did not find a positive relationship between a species' temperature of maximal activity and its degree of behavioural dominance in the ant assemblage inhabiting an olive orchard in central Italy, and – contrary to what might be expected from a dominance-thermal tolerance trade-off – dominants were active at a wider range of temperatures than subordinates. As these authors discussed, the absence of a trade-off could be due to the subset of ants they examined. They focused on the interactions that occurred in the trees, not on the ground. Olive trees seemed to provide shaded foraging patches: Temperature variation was not especially great and maximum temperatures were not very high (36°C in summer). The dominance-thermal tolerance trade-off is not necessarily expected to be present if temperatures are not highly variable. In contrast, they suggested the results could have been different if they had looked at ants foraging on the ground, since mowing practices exposed the soil between trees and thus created much hotter microhabitats (SANTINI & al. 2007). Indeed, the influence of this type of trade-off on ant coexistence may be contingent on the environmental context (WIESCHER & al. 2011).

In some cases, thermal tolerance gives a competitive advantage to invasive species: in New Zealand, the native *Pheidole rugosula* occupies more baits when temperatures are between 20°C and 30°C, and the invasive *Monomorium sydneyense* dominates when temperatures are between 30°C

and 40°C (STRINGER & al. 2007). However, the scavenging performance of the Argentine ant (*Linepithema humile*) in Doñana National Park (Spain) is reduced at high summer temperatures, when the native species are highly efficient at collecting arthropod corpses (ANGULO & al. 2011). In fact, tolerance to local abiotic factors, such as temperature or moisture, plays a key role in determining Argentine ant invasion around the world (HOLWAY & al. 2002, MENKE & HOLWAY 2006, WETTERER & al. 2006, ROURA-PASCUAL & al. 2011).

All these pieces of evidence raise an important question: Have the thermophilic activity patterns displayed by many subordinate species in arid environments evolved as a mechanism to avoid competition with dominant ants? Although it has been suggested that the physiological, morphological, and behavioural specializations of hot-climate specialists are indicative of a long evolutionary history of association with behaviourally dominant ants (ANDERSEN 1995), this is not the case for hot-climate specialists in the Mediterranean region, notably species in the genus *Cataglyphis* (see CERDÁ & RETANA 1997, 2000), *Proformica* (FERNÁNDEZ-ESCUDERO & TINAUT 1998), and *Formica* (see CAVIA MIRAVALLES 1988). The thermophilic activity patterns of these species do not seem to be a consequence of avoiding competition with dominant species; instead, increased heat tolerance seems to be an adaptation to hot environments (CERDÁ & al. 1998a). Thermophilic species are highly specialised for foraging during the hottest time of the day, but hardly interact with dominant species. However, heat tolerance may have evolved in response to competitive interactions with behaviourally dominant ants in relatively mesic environments, permitting subordinate ants to use thermally unfavourable times for competitor-free foraging, and thus secondarily invade arid zones (BESTELMEYER 1997). This extreme behaviour may also relate to a highly specialised diet: Ants of extreme climates are all scavengers that exploit prey killed by the heat or cold, and their foraging success increases at extreme temperatures (HÖLLDOBLER & TAYLOR 1983, BESTELMEYER 1997, CERDÁ & al. 1998a, b).

The dominance-discovery trade-off and its modulation by parasitoids

Classically, two main types of competition have been distinguished in animals: exploitative and interference. Exploitative competition involves the ability of species to find and use resources before others. Interference competition involves the ability of species to prevent resource use by others (or to expulse them from the resource) either directly by aggression or indirectly by maintaining a territory (FELLERS 1987). WILSON (1971) was the first to distinguish opportunist ant species specialised in exploitative competition (discovering food quickly and exploiting it before other ants arrive) from extirpators specialised in interference competition (dominating food aggressively). Later, FELLERS (1987) similarly categorised North-American woodland ants: Some species that were aggressive and behaviourally dominant used interference competition, and those that were less aggressive and subordinate used exploitative competition. The most interesting result of FELLERS' (1987) study was the inverse relationship observed between dominance at baits and the relative speed with which baits were found. The less aggressive subordinate

species located and exploited food quickly, thus circumventing interference by aggressive and behaviourally dominant species (FELLERS 1987). It was the first description of the dominance-discovery trade-off, another of the compensatory mechanisms that counter the effects of competition and promote local coexistence of ant species (FEENER & al. 2008). PARR & GIBB (2009, 2012) consider the dominance-discovery trade-off to be the most widely cited ecological trade-off relating to competition and coexistence in ant assemblages. However, this trade-off is controversial: For instance, LESSARD & al. (2009a) found no evidence of the dominance-discovery trade-off in essentially the same ant species assemblage that FELLERS (1987) used. Moreover, PARR & GIBB (2012), combining a literature review and meta-analysis with experimental work, concluded that the assumption that this trade-off is widespread appears to be incorrect and demands closer inspection. Unfortunately, this "closer inspection" exceeds the aims of our review.

Edward G. LeBrun (pers. comm.) highlights some methodological problems to test the dominance-discovery trade-off hypothesis: "Firstly, it is necessary to measure also the species prevalence within the habitat, and many tests of this hypothesis (e.g., PARR & GIBB 2012) do not factor out prevalence. If foraging success is driven entirely by chance processes, highly prevalent species will both discover and dominate a large fraction of the resource base, and low prevalence species will do the reverse. Therefore, the null expectation for a "trade-off" curve between dominance and discovery ability (when the traits are measured in a manner that does not factor out prevalence) is a positive relationship. If a dominance-discovery trade-off process operates, then assemblages measured in this way may show no relationship: The negative relationship between dominance and discovery cancelling the inherent underlying positive association driven by prevalence. Secondly, by its nature, this hypothesis applies only to directly competing species and thus is a second order explanation for maintaining species diversity in ant assemblages. Species that have evolved separate foraging niches (e.g., thermal foraging profiles) would not be expected to adhere to a dominance-discovery trade-off curve as they do not occupy the same patch of niche space. Thus studies that look for this relationship in thermally challenging environments and do not find it, are not providing strong tests of the hypothesis."

In their bibliographic review, PARR & GIBB (2012) observed that the dominance-discovery trade-off is only detected in systems in which parasitoids are present, namely decapitating phorid flies. These phorids are species-specific and may affect colony fitness. The influence of parasitoids on this trade-off has been extensively studied in New World ant assemblages that include invasive species, either in their native or introduced range (ORR & al. 1995, ORR & SEIKE 1998, FEENER 2000, FEENER & al. 2008), and in assemblages free of invasives (LEBRUN & FEENER 2002, 2007, ORR & al. 2003, LEBRUN 2005). Linked to the dominance-discovery trade-off, a second trade-off occurs between the ability of an ant species to dominate food resources and its ability to avoid direct and indirect reduction of fitness by parasitoids (LEBRUN & FEENER 2007). When linear dominance hierarchies exist, the presence of phorid flies eliminates the linearity of dominance, reduces the competitive asymmetries between the host (a dominant species) and its subdominant competitors, and therefore increases the uncertainty of competitive outcomes (LEBRUN 2005). In the Chiricahua Mountains (USA), LEBRUN & FEENER (2007) observed a dominance-discovery trade-off among seven non-host species, but this trade-off disappeared when all nine (seven non-host + two dominant host) species interacted in the absence of phorids. When a host species was attacked by phorids, the response was to reduce the number of workers harvesting food sources, and thus the ability to dominate baits was decreased. When not subject to phorid attacks, a host species' level of dominance was greater relative to its discovery ability and thus violated the trade-off. Thus, in these assemblages, behavioural changes by dominant species (inducible defensive responses against parasitism) maintain the dominance-discovery trade-off (LEBRUN & FEENER 2007).

Habitat complexity

Ecological theory sustains that resources may be more finely divided in more complex environments, resulting in a wider diversity of potential niches and thus richer flora and fauna (PUTMAN 1994). Vegetative structure is among the main factors that affect habitat complexity, and it is also one of the main factors affecting the composition and structure of ant communities (BESTELMEYER & WIENS 1996, WANG & al. 2001, LASSAU & HOCHULI 2004, ARNAN & al. 2007, KLIMES & al. 2012). It may indirectly modify interspecific interactions across the gradient of habitat complexity (RETANA & CERDÁ 2000, ARNAN & al. 2009). Thus, in Spanish Mediterranean ecosystems, when habitat complexity increases (from open habitats to closed-canopy forests), dominant species become more abundant and ant richness declines (RETANA & CERDÁ 2000). Similarly, the number of species may decline in more shaded habitats in semi-arid zones of Australia because the regional ant fauna consists largely of taxa adapted to open habitats (ANDERSEN 1992, 1995). Reduced vegetative structure resulting from disturbance (see the next section) may also enhance ant diversity by increasing habitat heterogeneity or microclimate favourability, or by reducing the activity of dominant species (BESTELMEYER & WIENS 1996). ARNAN & al. (2009) found that habitat structure played an important role in structuring ant communities by making habitat less favourable for dominant territorial species of the *Formica rufa* group. In the Spanish Pyrenees, dense forests are the most favourable forest type for *F. lugubris*, whose abundance negatively affects that of other ant species in the community. Habitat complexity may also influence the dominance-discovery relationship. PARR & GIBB (2012) observed a weaker relationship between dominance and discovery in complex habitats; substrate heterogeneity might alter interspecific interactions and prevent resource monopoly by dominant aggressive species.

Relatively little is known about the influence of microhabitat diversity on resource use in ant communities. In the Chiricahua Mountains (Arizona, USA), WILKINSON & FEENER (2007) observed that habitat complexity (with or without leaf-litter) modified ant-parasitoid interactions, and affected the competitive relationships between two behaviourally dominant species, *Pheidole diversipilosa* and *P. bicarinata*. In a coffee agroecosystem in Colombia, ARMBRECHT & al. (2004) examined the correlation between the

diversity of twigs in the leaf litter and the diversity of twig-nesting ants. They experimentally showed that microhabitat diversity (i.e., twigs) promoted ant diversity. In Neotropical wet forests (a highly heterogeneous habitat), the frequency of bait monopoly is associated with microhabitat type, monopoly by ants being more common in deep leaf litter than in shallow litter (MCGLYNN & KIRKSEY 2000). In the litterfall of the tropical forest floor, there are at least two different habitats for ants: the shallower, more exposed, and less rough upper surface formed by dead leaves, and the deeper, rougher interstices inside the litter. Large ant species are more efficient at reaching resources in the former, whereas small ants are more efficient in the latter (FARJI-BRENER & al. 2004). Thus, the ability to explore environmental interstices and crevices may constitute a competitive advantage for small ants as it could reduce potential competition with larger ants (FARJI-BRENER & al. 2004).

Disturbances

It has been suggested that habitat disturbance often favours behaviourally dominant ants (HOFFMANN & ANDERSEN 2003). In Doñana National Park, the invasive Argentine ant is competitively superior to the native ants, thanks to disturbances caused by human settlements, which provide food as well as shelter against thermal stress (CARPINTERO & al. 2003, ANGULO & al. 2007). Invasive ants may act as a disturbance force themselves. In California, competitively structured ant communities were dissembled, i.e., characterized by weak or random species co-occurrence, following Argentine ant invasion (SANDERS & al. 2003b). Similarly, in the eastern United States, ant communities invaded by the red fire ant, *Solenopsis invicta*, demonstrated a random pattern of species co-occurrence, while, in uninvaded sites, species co-occurred less often than expected by chance (GOTELLI & ARNETT 2000). While the presence of invasive fire ants has frequently been associated with a decline in native ant diversity and abundance (e.g., in central Texas, LEBRUN & al. 2012), invasion is also often coupled with habitat disturbance (TODD & al. 2008, STUBLE & al. 2009 and references therein, but see LEBRUN & al. 2012). Indeed, KING & TSCHINKEL (2006) experimentally demonstrated in a pasture in Florida that *S. invicta* does not suppress local ants (that were mostly introduced tramp species): The low diversity and abundance of local ants in degraded ecosystems may result from a prior disturbance, not from interaction with fire ants (KING & TSCHINKEL 2006). These examples illustrate how environmental disturbance may change ant community structure by allowing or favouring the arrival of a dominant and, in these cases, invasive species (see KRUSHELNYCKY & al. 2009 for more examples and a review of the role of disturbance on ant invasion processes). Two recent works (UNDERWOOD & FISHER 2006 and PHILPOTT & al. 2009) have reviewed and summarized studies concerning the effect of environmental disturbance on ant communities. We briefly discuss the effect of three disturbance processes, fire, flooding, and the creation of treefalls gaps, on competitive relationships.

Fire

Fire is one of the most important natural disturbances in many ecosystems, and its occurrence has significant implications for the structure and composition of plant and animal communities (GILL & al. 1981). Fire directly elimi-nates ants that nest in the vegetation, but not those that nest in the ground (ARNAN & al. 2006, FRIZZO & al. 2012). As a consequence, fire affects the structure and composition of ant communities indirectly, by simplifying habitat complexity and thus modifying the competitive interactions among species (ANDERSEN 1991, RETANA & CERDÁ 2000, YORK 2000, ARNAN & al. 2009; see also the previous section "Habitat complexity").

The effects of fire on dominant ants and behavioural dominance are poorly studied, and the few existing studies suggest that they depend on the biogeographical context. Most of the research on this topic comes from Australia. HOFFMANN & ANDERSEN (2003) extensively reviewed the response of ants to disturbance in Australia, and they mainly found that fire caused dominant Dolichoderinae to increase in forests. In subtropical Northern Australia, ANDERSEN & al. (2007) found that the abundance of the territorial, dominant species of *Iridomyrmex* was promoted by fire, whereas that of another territorial genus, *Oecophylla*, declined. In another study in the same region, PARR & ANDERSEN (2008) found that changes in competitive interactions at baits were dependent on vegetation. Fire caused dramatic declines in dominance of the patchily distributed, forest-associated species *Oecophylla smaragdina* and *Papyrius* sp., but had no effect on the overall dominance of open-savannah species *Iridomyrmex*. In turn, in another study conducted in the western Mediterranean Basin (X. Arnan & al., unpubl.), the relative abundance of dominant (sub-dominants at the global scale) ants increased with fire. However, two studies that examined the structure of ant communities a few years after fire, one in the Mediterranean Basin (ARNAN & al. 2007) and the other in the Siskiyou mountains in the USA (SANDERS & al. 2007a), found no evidence of competition, i.e., ant species in the communities were not organized in linear dominance hierarchies.

Flooding

For ground-dwelling ants, annual flooding may have dramatic effects on colonies. Even in ants that have nests that are well-adapted to resist annual floods, as in the European *Cardiocondyla elegans*, up to 40% of colonies may be lost during winter floods (LENOIR 2006). Differences in flood tolerance have been found in some Amazonian *Pheidole* species (MERTL & al. 2010). At the community level, the density, richness, and community composition of litter-nesting ants are negatively impacted by flooding (MERTL & al. 2009). However, low levels of flooding play a role in the maintenance of tropical ant diversity. Infrequently flooded habitats contain a mixture of litter-nesting species from distinctly different communities: Those that are found in non-flooded forest and those that occur in highly flooded forest. Such habitats may thus serve as a refuge from competition for otherwise rare species (MERTL & al. 2009).

Thus, flood tolerance may trade-off with dominance: Dominant species are infrequent in flood-prone ant communities (but see the studies about *Solenopsis invicta*, whose colonies form rafts after flooding, e.g., HAIGHT (2006), TSCHINKEL (2006)). In some Austrian floodplains, ant assemblages are shaped by environmental disturbance rather than interspecific interactions. These assemblages lack top competitor species, and the most abundant species is *Myrmica rubra*, which is highly tolerant of flooding (SCHLICK-STEINER & al. 2005). In the floodplains of pristine rivers in

the Alps (Central Europe), LUDE & al. (1999) found that nine ant species are able to survive floods. *Formica selysi* colonises and attains its highest nest densities on unvegetated gravel islands and bars. Following flooding, 72% of the *F. selysi* colonies had survived. In these areas, floods are probably crucial in providing suitable habitat for those ant species that live in unvegetated habitats. In Australia, the species that successfully inhabit flood-prone environments have flexible reproductive habits, which may provide a competitive advantage by allowing rapid replacement of lost colony biomass after a flood event (BALLINGER & al. 2007).

Forest gap dynamics

Habitat structure and complexity are different in forest gaps, as may be ant communities. Forest gap dynamics can arise from natural disturbance, such as tree falls, and human disturbance, such as logging. Both disturbance types change environmental conditions drastically. Some studies have not found an important effect of tree fall on ant communities. FEENER & SCHUPP (1998) found little evidence that ant assemblages were different in treefall gaps that formed in a Panamanian moist lowland forest; and PATRICK & al. (2012) showed that treefall gap dynamics have a limited role in promoting ant diversity in a tropical montane cloud forest in Costa Rica. However, other studies have found evidence of an effect of tree fall on ants. In an Indian primary rainforest, BASU (1997) recorded more species in the closed canopy forest than in treefall gaps. In SE Asian lowland forest, anthropogenic disturbances reduced biodiversity and changed ant community structure (FLOREN & LINSENMAIR 2001). Ant communities of these disturbed forests are saturated, with only a few species dominating them. Even in a 40-year-old forest, where ant communities were more similar to those of primary forest, the effects of anthropogenic disturbance were still evident, demonstrating how long ant communities take to recover (FLOREN & al. 2001, FLOREN & LINSENMAIR 2005). In this system, ant assemblages in primary forests were not significantly different from randomly assorted communities (i.e., not structured by competition), whereas those in disturbed forests showed a clear deterministic pattern. These changes may indicate that structuring mechanisms in these habitats are different, with predominantly deterministic processes operating in disturbed forests versus stochastic processes in mature forests (FLOREN & LINSENMAIR 2001, 2005).

In northern Europe, modern forest management has created new types of successional habitat and habitat mosaics. PUNTTILA & al. (1991) compared ant assemblages in mature forests (over 120 years in age) and in areas cleared zero, two, and ten years ago. They concluded that wood-ant systems in old forests are destroyed when clear-cutting occurs, probably because of the loss of food resources. In older boreal forests, the structure of ant communities was largely determined by top competitors, the territorial species of the wood-ant group (*Formica aquilonia* and *F. lugubris*), whereas, in younger clearcuts, the top competitor was the aggressive slavemaking ant *F. sanguinea* (PUNTTILA & al. 1996). In southern Europe, in the Pyrenees Mountains, ARNAN & al. (2009) studied the effect of different pine forest management strategies on ant communities. They found that *F. lugubris*, the top competitor, was much less abundant in naturally regenerated forests in nature re-

serves than in even-aged stands. Forests with high tree density were most favourable for *F. lugubris*, whose abundance negatively affected that of the other ant species in the community (ARNAN & al. 2009).

Predation

According to FEENER (2000), a consequence of the overwhelming evidence for competition in ant communities is that the roles of such "top-down" processes as predation and parasitism have been ignored. Ants are potentially one of the most easily available prey for predators, because they are common and predictable targets for both vertebrates (e.g., lizards, frogs, birds, or mammals) and invertebrates (e.g., spiders and several insect groups, including but not limited to antlions and myrmecophagous ants). In general, ant mortality caused by predators is light (MACKAY 1982), although in some cases the losses may be substantial, as in a *Cataglyphis bicolor* population in Greece, where estimated losses due to spider predation were as high as 1% of forager abundance per night (HARKNESS 1977). Predation may cause colonies of desert seed-harvesters or scavengers to cease surface activity for extended periods of time (WHITFORD & BRYANT 1979, WEHNER & al. 1992), or decrease ant forager abundance and nest density (GOTELLI 1996). However, there is little evidence that predation affects entire ant populations. The only study at the population level is that of RAO (2000). He experimentally assessed the impact of predation by armadillos on incipient and young *Atta* colonies in the Lago Guri islands (Venezuela), and his results suggest that predation influenced nest densities.

Predation has thus not been considered to be an important organizing force in ant communities. Nevertheless, some studies suggest that invertebrate predators can have impacts on the distribution, abundance, and behaviour of ground-foraging ants that resonate throughout the community (GOTELLI 1996). Vertebrate predators have been shown to similarly affect ant communities (RISSING 1981, WANGER & al. 2011). The risk of predation may be higher for certain species within a given assemblage, thus decreasing their abundance and potentially affecting local competitive outcomes. Different studies have found that ant-eating predators may only feed on some genera or species: In Slovakia, *Zodarion germanicum* preys mainly on dominant or sub-dominant Formicinae (*Lasius* and *Formica*) (PEKÁR 2004, PEKÁR & al. 2008), whereas in California, horned lizard adults predominately eat the largest ant species (*Pogonomyrmex* and *Messor*), juveniles focus on smaller species (*Crematogaster* and *Pheidole*), and both adults and juveniles prefer native ants to the smaller invasive Argentine ant (SUAREZ & al. 2000). Overall, the effect of predators may be similar to that of phorid flies (see the section above: "The dominance-discovery trade-off and its modulation by parasitoids"), differentially affecting dominant and subordinate species and thus modifying competitive relationships.

Relationships between richness and dominance in ant communities in different biogeographical areas

The next step is to determine if dominance and species richness are related in different biogeographical areas. When considering species richness alone, local ant species richness is asymmetrical along a latitudinal gradient; the maximum number of ant species is found in the tropics (Tab.

S1) and diversity is higher in the southern versus the northern hemisphere (DUNN & al. 2009). The local richness of ants in tropical rainforests around the world is astonishingly high: Around 100 - 300 or more ant species (occasionally more than 500; BRÜHL & al. 1998) have been identified in the tropical forests of Asia, Africa, and South America (HÖLLDOBLER & WILSON 1990). In contrast, the abundance of dominant species in rainforests is much lower than in tropical and subtropical woodlands (Tab. S1), tropical tree plantations, or forests, where ant mosaics, with dominants distributed horizontally in the upper canopy strata, are frequently found (MAJER & al. 1994, PERFECTO 1994, DAVIDSON & al. 2007). In other biogeographical regions, species richness varies more at the continental scale than at the local scale (e.g., across habitats). For instance, species richness was generally higher in habitat types sampled in Australia than in their counterparts in the Northern hemisphere (ANDERSEN 1997, 2003). Paradoxically, the extraordinary species richness of Australia's open habitats correlates with high levels of behavioural dominance (see below), and both species richness and the abundance of behaviourally dominant ants in arid, semi-arid, and seasonally arid Australia are much higher than in comparable environments elsewhere in the world (ANDERSEN 1997, 2003). Species richness is lowest in boreal, cold-temperate forests. Studies conducted in the taiga biome commonly conclude that top competitors of the genus *Formica* act as "organizing centres" of the community (SAVOLAINEN & VEPSÄLÄINEN 1989). In cold-temperate communities lacking these territorial species, or in temperate areas, the number of ant species increases, and dominants are less abundant (Tab. S1). In North American deserts (ANDERSEN 1997) and in the Australian arid zone (ANDERSEN 1993), dominant Dolichoderinae are almost universally present. Generalised Myrmicinae, which are competitively subdominant to *Iridomyrmex* throughout most of their range (ANDERSEN 1995), can be highly abundant at heavily shaded sites in warm climates in Australia and the USA (ANDERSEN 1997), as well as in Mediterranean forests (CERDÁ & al. 1997). In open Mediterranean areas and in deserts in other areas of the world, interspecific competition is likely to be less important than temperature in structuring ant communities (CERDÁ & al. 1997, 1998a) (as described in the section "The trade-off between dominance and thermal tolerance"). When DUNN & al. (2009) analysed global patterns of ant species richness, they found that richness seemed to be lowest in California chaparral and the Gobi desert.

A continent-wide analysis of Australian communities revealed a seemingly paradoxical positive linear relationship between the abundance of behaviourally dominant species and local species richness (ANDERSEN 1995). At local scale, ARNAN & al. (2011) recently examined the fine-scale spatial distribution of ants in an Australian tropical savannah in order to clarify the mechanisms underlying this broader pattern. Indeed, they found a positive relationship between the abundance of dominant species and the richness of subordinate species. They suggest that dominant species may actually promote species richness by neutralizing the effects of subdominant ants on subordinates and that the "protection" exerted by dominants can help explain the more general positive correlation between functionally dominant ants and species richness throughout Australia. This relationship and the proposed "neutralising" mecha-

nism may also be present in Finnish ant communities (Kari Vepsäläinen, pers. comm.). As ANDERSEN (1995) suggests, this correlation, present in at least some parts of Australia, directly contradicts HÖLLDOBLER & WILSON's (1990) "dominance-impoverishment rule", which states that an inverse relationship exists in ant communities between species richness and the degree of behaviourally competitive dominance that species demonstrate.

Approaches used to discern if and how competition is structuring ant communities

It is not trivial work to conclusively demonstrate the effects of competition on biological communities (e.g., CONNELL 1983, SCHOENER 1983, UNDERWOOD 1986), especially in the field, where it is inherently difficult to control external factors. An array of different kinds of studies have been conducted, all attempting to address the effect of the competitive pressure exerted by dominant species on ant communities. In this section, we summarize the main types of methodologies that have been used (Tab. 2). The most straight-forward studies examine the co-occurrence and spatial distribution of species with data from pitfall traps or baits (e.g., JACKSON 1984, FELLERS 1987, ANDERSEN 1992, ADAMS 1994, MORRISON 1996, CERDÁ & al. 1997, BESTELMEYER 2000, RETANA & CERDÁ 2000, SANDERS & al. 2003a, ARNAN & al. 2009, 2011). A particular subset of these studies focus on the numerous species of tropical arboreal ants, which are often arranged in a mosaic such that dominant species have mutually exclusive distributions among trees (e.g., ROOM 1971, MAJER 1972, JACKSON 1984, ADAMS 1994, DEJEAN & al. 1997, BLÜTHGEN & al. 2000, FLOREN & LINSENMAIR 2000, BLÜTHGEN & STORK 2007, DAVIDSON & al. 2007, SANDERS & al. 2007b). In general, these observational studies seemingly yield evidence of interspecific competition, especially among dominant species. However, these studies have also received much criticism. The main criticism is that it is hardly possible to suggest the operation of interspecific competition based solely on species distribution data: The fact that species do not co-occur does not necessarily imply interspecific competition is taking place. This is a problem shared by baiting experiments that focus on ant behaviour. Evidence for the regulation of small-scale diversity by dominant ants often comes from such experiments, which examine the numbers of species present at a food resource at a given time ("momentary" diversity) and the interactions that take place (e.g., FELLERS 1987, ANDERSEN 1992, CERDÁ & al. 1997, RETANA & CERDÁ 2000, PARR 2008). First, agonistic behaviour observed between individuals belonging to a pair of species does not necessarily imply interspecific competition is taking place, because competition is a process of populations, not of individuals (e.g., VEPSÄLÄINEN & PISARSKI 1982, RIBAS & SCHOEREDER 2002, GIBB & HOCHULI 2003). Second, exclusion from baits does not necessarily equate to competitive exclusion at the community level, such that competition needs to be invoked as a key structuring mechanism (e.g., ANDERSEN & PATEL 1994, SANDERS & GORDON 2000, RIBAS & SCHOEREDER 2002, GIBB & HOCHULI 2003).

More recently, it has been suggested that the processes underlying ant community structure should be more explicitly examined using analyses that infer cause and effect (e.g., ANDERSEN & PATEL 1994, RIBAS & SCHOEREDER 2002), including the experimental removal or introduction

Tab. 2: Main types of methodologies used in studies addressing the effects of competition on ant communities.

Methodology	Description	Examples
Pitfall trapping	Examination of the spatial distribution of species inferred from ant presence and abundance in pitfall traps	Bestelmeyer & Wiens (1996), Basu & al. (1997), Cerdá & al. (1997), Parr (2008), Arnan & al. (2007, 2009, 2011)
Baiting experiments	Examination of the dominance behaviour and spatial / temporal distribution of species inferred from ant presence, abundance, and interaction at a bait at a given time	Fellers (1987), Andersen (1992), Morrison (1996), Cerdá & al. (1997), Retana & Cerdá (2000)
Manipulative experiments	Examination of ant community structure (by pitfall trapping or baiting) prior to and following experimental manipulation of dominant species presence (removal or introduction)	Andersen & Patel (1994), Gibb & Hichuli (2004), King & Tschinkel (2006, 2008), Gibb (2005, 2011), Gibb & Johansson (2011)
Null model analysis	Comparison of the observed pattern of species distributions in a presence-absence or abundance matrix (from data obtained through pitfall trapping or baiting) to the pattern present in random matrices	Floren & Linsenmair (2000), Gotelli & Ellison (2002), Ribas & Schoereder (2002), Sanders & al. (2007a, b), Wittman & al. (2010), Cerdá & al. (2012), LeBrun & al. (2012)

of dominant ants (e.g., Andersen & Patel 1994, Gibb & Hochuli 2003, 2004), or simulations based on null models (Floren & Linsenmair 2000, Floren & al. 2001, Gotelli & Ellison 2002, Ribas & Schoereder 2002, Sanders & al. 2003b, 2007a, Cerdá & al. 2012). The need for experimental testing of the importance of competition has long been recognised in ecology (Connell 1983, Schoener 1983, Underwood 1986). Given their inherent practical difficulty, manipulative experiments are not widespread in the ant literature (Yasuno 1965, Andersen & Patel 1994, Perfecto 1994, Gibb & Hochuli 2004, Gibb 2005, King & Tschinkel 2006, 2008, Gibb 2011, Gibb & Johansson 2011). They consist of the removal or introduction of one or more ecologically dominant ants from a community; the structure of the ant community before and after the experimental manipulation is then characterised. Most research of this type has "removed" ant colonies, either by fencing (e.g., Andersen & Patel 1994, Sanders & Gordon 2003), caging (Gibb 2003, Gibb & Hochuli 2004), extermination via insecticides or boiling water (e.g., Perfecto 1994, Gibb 2005, King & Tschinkel 2006, LeBrun & al. 2007), or unearthing them, performed in tandem with the previous methods (e.g., Kugler 1984, Gibb 2011, Gibb & Johansson 2011, digging + insecticide). A few studies involve the introduction of dominant species where they did not previously occur or after defaunation (e.g., Simberloff & Wilson 1969, Cole 1983, Rosengren 1986, King & Tschinkel 2008). Interestingly, most of these studies reveal that dominant species have limited effects on ant assemblages (but see Yasuno 1965, Gibb 2011). However, this work has also attracted its share of criticism. Firstly, most experiments are relatively short (e.g., Parr 2008), usually not lasting longer than a year, a time period over which the effects of competition might not yet manifest themselves. Secondly, removal experiments usually target only one dominant species, when a system may harbor several, and thus the effects of competition at the assemblage level may be masked (e.g., Gibb & Hochuli 2004). Moreover, when the removal technique kills ants, the dead workers produced may provide an important food source for some ant species and thus promote population growth (e.g., Gibb 2011). Also, even if no change is seen at the community level, particular species may response positively. This response may be due less to the relaxation of competitive pressures imposed by dominant species and more to other causes. For instance, dominant ants might suppress ant predators.

As for null models, they are one of the latest and most mathematically explicit techniques used to examine species co-occurrence patterns and, consequently, evaluate if deterministic assembly rules, such as those resulting from competition, may be at work in communities (e.g., Gotelli & Graves 1996, Gotelli 2000, 2001). For null-model procedures, see Gotelli & Graves 1996. Many papers have been published in the last decade that use and address the use of this approach with ant assemblages (e.g., Gotelli & Arnett 2000, Albrecht & Gotelli 2001, Gotelli & Ellison 2002, Ribas & Schoereder 2002, Sanders & al. 2003b, 2007a, Parr & al. 2005, Dunn & al. 2007, Wittman & al. 2010, Baccaro & al. 2012, Cerdá & al. 2012). It is worth noting that the application of null models in ecology has demonstrated that many of the spatial distribution patterns that have been attributed to local deterministic processes can actually arise independently of them (Gotelli 2000, 2001) and may well be a consequence of regional-scale processes. Although we cannot doubt that the application of these models has led to great progress in community ecology, null models do not indicate whether a deterministic process is actually at work (e.g., Ribas & Schoereder 2002). Instead, they should be considered to test the null hypothesis of species co-occurrence being attributable to stochasticity. Thus, if this null hypothesis can be rejected, co-occurrence can be said to be framed by biological as opposed to random processes. However, it nonetheless remains to be demonstrated that the biological process operating is competition. For instance, checkerboard patterns can also be attributed to species' preferences for different abiotic conditions (e.g., Morrison 1996), as well as mutualism or predation (Underwood 1986). Only after rejecting these alternative hypotheses can one suggest competition as a structuring force in ant assemblages (Ribas & Schoereder 2002). Another issue is that deterministic chaos can also generate random community patterns (Bascompte & Solé 1995, Floren & Linsenmaier 2001, Floren & al. 2001). In fact, Vepsäläinen & Pisarski (1982) criticized the application of null models early on. They argued that it is only sensible to test for competition after all known differences in species' biologies have been accounted for. That is, a realistic null competition model does not predict randomly assembled com-

munities, but competition may fortuitously organise communities such that the outcome fits a random pattern. An increasing number of studies are also using null models to infer the effects of competition using an examination of the phylogenetic structure of communities (LESSARD & al. 2009b, MACHAC & al. 2011) as well as patterns of temporal overlap (ALBRECHT & GOTELLI 2001, DUNN & al. 2007, WITTMAN & al. 2010, STUBLE & al. in press). Few works using this approach support a strong role for competition (GOTELLI & ARNETT 2000, SANDERS & al. 2003b, PARR & al. 2005, PARR 2008, LESSARD & al. 2009b, MACHAC & al. 2011 only at low-elevation sites), whereas many more suggest it is of limited importance (e.g., RIBAS & SCHOEREDER 2002, SANDERS & al. 2007a, WITTMAN & al. 2010, MACHAC & al. 2011 at high-elevation sites, BACCARO & al. 2012, CERDÁ & al. 2012, STUBLE & al. in press).

In conclusion, despite it being difficult to conclusively demonstrate the effects of competition in ant communities, there is considerable indirect support for its importance. This corroboration includes the spatial patterns of species distributions (ARNAN & al. 2009, 2011), including the existence of spatial ant mosaics (ROOM 1971, MAJER & al. 1994, BLÜTHGEN & al. 2000), the limitations placed on the foraging success of subordinate species at local food resources by dominant species (e.g., FELLERS 1987, SAVOLAINEN 1991, ANDERSEN 1992, ANDERSEN & PATEL 1994, MORRISON 1996, CERDÁ & al. 1998b, GIBB 2005), behavioural dominance hierarchies (SAVOLAINEN & VEPSÄLÄINEN 1988), territoriality (FOX & al. 1985, ANDERSEN & PATEL 1994), agonistic behaviour (ANDERSEN & al. 1991) and results from null model testing (PARR & al. 2005). However, experimental evidence and model simulations suggest that the operation of interspecific competition does not necessarily mean it is regulating broader foraging abundance and, consequently, preventing species co-occurrence at the assemblage level (e.g., ANDERSEN & PATEL 1994, RIBAS & SCHOEREDER 2002, GIBB & HOCHULI 2004, KING & TSCHINKEL 2006, 2008, DUNN & al. 2007, SANDERS & al. 2007a, GIBB & JOHANSSON 2011, BACCARO & al. 2012). Moreover, LESSARD & al. (2012) have recently shown that climate and biogeographic history are more important than competition in shaping ant communities. The role of competition in structuring ant assemblages may be more limited than previously thought.

Some open issues

Twenty years ago, HÖLLDOBLER & WILSON (1990) wrote: "We are persuaded that the mechanisms we know of today represent only a fraction of the processes that actually exist. We also believe that the bottom-to-top approach is the best way to understand communities. In other words, it is best to start with the identification of the processes in individual species and proceed to a simulated synthesis of the community." Four years ago, PARR & GIBB (2009) wrote: "Given the potential importance of competition in structuring local assemblages, the impact of disturbances (natural and anthropogenic) on competition and dominant ants deserves more attention." It will always be difficult to use only one ecological process to explain variation in the wild. In spite of this difficulty, competition has frequently been evoked as the strongest, most significant hallmark of ant community ecology, even though this interpretation appears to be categorically wrong. Thirty years ago, VEPSÄLÄINEN

& PISARSKI (1982) clearly stated that competition is just one of many important factors or mechanisms affecting the assembly structure of ants. Their message is as equally valid now as it was then. Some ant ecologists (e.g., RIBAS & SCHOEREDER 2002, ANDERSEN 2008) have already abandoned the notion that a single monolithic process governs community organization. It is obvious that competition is at work in many ant communities across different habitats, but it is also a platitude that this effect is poor or remains unclear in many other habitats distributed throughout the world. Although we cannot deny the importance of competitive processes in modulating ant communities, this review challenges the idea that competition is a significant hallmark of ant community ecology. Indeed, it presents evidence that competition is much less important than previously thought, namely research that shows that, in many situations, competitive dominance may be replaced or have its impact mediated by other abiotic or biotic mechanisms (see the section "Factors affecting competition", and also ANDERSEN 2008). Indeed, most modern, rigorous analyses fail to find evident effects of competition. More studies, both local and global, of ant communities are needed to elucidate the complex interactions that modulate ant community structure in different biogeographical areas, with the ultimate goal being to understand processes and patterns, and thus build a solid theory of ant community ecology.

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Digital supplementary material to

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Tab. S1: Structural features of ant communities from different biogeographical areas. [a] All sites were sampled with pitfall traps or counting ants in quadrats except: # count of the number of nests, [*] baits. [b] Dominant taxa include species of *Iridomyrmex*, *Formica* (*rufa*, *exsecta*, *microgyna* groups), *Oecophylla*, *Azteca*, *Pseudomyrmex*, army ants (*Eciton*, *Labidus*, *Dorylus* or *Aenictus*), leaf-cutting ants (*Atta*, *Acromyrmex* and other Attini), and tramp species such as *Linepithema humile* or *Solenopsis invicta*.

	SITES [a]	N of species	% Dominant species [b]	% Abundance of dominant species [b]	% Abundance of two most common species	Reference
	COLD-TEMPERATE FORESTS					
1	Young taiga clearcut (Finland)	18	28	62	65	PUNTTILA & al. (1996)
2	Old taiga clearcut (Finland)	19	26	67	77	PUNTTILA & al. (1996)
3	Mature taiga forest (Finland)	8	13	94	97	SAVOLAINEN & VEPSÄLÄINEN (1989)
4	Spruce forest (Switzerland)	5	20	94	98	CHERIX & BOURNE (1980)
5	Mixed-hardwood forest (USA) #	13	0	0	68	HERBERS (1989)
6	Mixed-hardwood forest (USA) #	8	0	0	80	HERBERS (1989)
7	Tall open forest (Australia)	18	11	17	62	ANDERSEN (1986a)
8	Tall open forest (Australia)	18	11	8	68	ANDERSEN (1986a)
9	Closed forest (Australia)	10	10	2	67	ANDERSEN (1986a)
	TEMPERATE FORESTS AND WOODLANDS					
10	Hardwood forest (USA)	16	0	0	48	LYNCH & al. (1988)
11	Open oak-juniper woodland (USA)	24	0	0	41	ANDERSEN (1997)
12	Oak-juniper woodland (USA)	30	3	6	26	ANDERSEN (1997)
13	Pine-oak woodland (USA)	22	0	0	25	ANDERSEN (1997)
14	Eucalyptus woodland (Australia)	47	18	2	48	ANDERSEN (1986b)
15	Heathland (Australia)	22	19	18	36	ANDERSEN (1986b)
16	Poplar forest [APo1] (Hungary)	10	10	0.14	89	ALVARADO & GALLÉ (2000)
17	Poplar forest [APo2] (Hungary)	12	8	0.15	87	ALVARADO & GALLÉ (2000)
18	Poplar forest [BuPo3] (Hungary)	18	17	15	78	ALVARADO & GALLÉ (2000)
19	Oak forest [AOa2] (Hungary)	10	10	2	79	ALVARADO & GALLÉ (2000)
20	Oak forest [BuOa3] (Hungary)	11	18	2	78	ALVARADO & GALLÉ (2000)
21	Juniper woodland [BuJu1] (Hungary)	12	0	0	70	ALVARADO & GALLÉ (2000)
22	Juniper woodland [BoJu2] (Hungary)	11	0	0	71	ALVARADO & GALLÉ (2000)
23	Juniper woodland [BoJu3] (Hungary)	12	0	0	46	ALVARADO & GALLÉ (2000)
24	Old pine forest (40 y) (Hungary)	15	20	78	78	ALVARADO & GALLÉ (2000)
25	Young pine forest (Hungary)	13	15	59	77	ALVARADO & GALLÉ (2000)
26	Open grassland (Poland) #	5	0	0	76	GALLÉ & al. (1998)
27	Shrubland (Poland) #	6	0	0	57	GALLÉ & al. (1998)
28	Pine forest [plot 8] (Poland) #	5	0	0	55	GALLÉ & al. (1998)

29	Pine forest [plot 9] (Poland) #	6	17	< 0.01	79	GALLÉ & al. (1998)
30	Open grassland (Hungary)	6	17	< 0.01	73	JÁRDÁN & al. (1993)
31	Closed grassland (Hungary)	10	10	3	93	JÁRDÁN & al. (1993)
32	Shrubland (Hungary)	10	10	35	90	JÁRDÁN & al. (1993)
33	Closed poplar forest (Hungary)	12	17	66	69	JÁRDÁN & al. (1993)
	MEDITERRANEAN AREAS					
34	Open grassland (Spain)	12	0	0	66	CERDÁ & al. (1997)
35	Open grassland (Spain)	13	0	0	58	CERDÁ & al. (1998)
36	Shrubland (Spain) #	22	0	0	48	JIMÉNEZ-ROJAS & TINAUT (1992)
37	Aleppo pine forest (Spain)	15	0	0	88	CERDÁ & al. (1997)
38	Aleppo pine forest (Spain) #	13	0	0	48	JIMÉNEZ-ROJAS & TINAUT (1992)
39	Holm oak forest (Spain)	15	0	0	84	CERDÁ & al. (1997)
40	Oak forest (Portugal) [*]	26	0	0	66	CAMMELL & al. (1996)
41	Pine forest (Portugal) [*]	23	0	0	58	CAMMELL & al. (1996)
42	Eucalyptus forest (Portugal) [*]	34	0	0	41	CAMMELL & al. (1996)
43	"Dehesa" pastureland) (Spain) #	20	0	0	54	REYES-LÓPEZ & al. (2003)
44	Dry grassland (Italy)	8	0	0	74	CASTRACANI & al. (2010)
45	Wet grassland (Italy)	13	0	0	67	CASTRACANI & al. (2010)
46	Pine forest (Italy)	13	0	0	82	CASTRACANI & al. (2010)
47	Mixed oak forest (Italy)	14	0	0	61	CASTRACANI & al. (2010)
48	Mediterranean scrubland (Italy)	9	0	0	43	CASTRACANI & al. (2010)
	ARID AND SEMI-ARID ZONES AND DESERTS					
49	Desert scrub (USA)	17	12	37	42	ANDERSEN (1997)
50	Desert scrub (USA)	24	8	23	26	ANDERSEN (1997)
51	Desert scrub (USA)	26	12	23	32	ANDERSEN (1997)
52	Open shrubland (Australia)	32	25	60	46	ANDERSEN (1993)
53	Mixed grassland (Australia)	39	10	33	42	ANDERSEN (1993)
54	Namib desert (South Africa)	13	0	0	62	MARSH (1985)
55	Forest steppe [transect 1] (Iran)	15	0	0	37	PAKNIA & PFEIFFER (2011)
56	Forest steppe [transect 2] (Iran)	15	0	0	44	PAKNIA & PFEIFFER (2011)
57	Forest steppe [transect 5] (Iran)	7	0	0	52	PAKNIA & PFEIFFER (2011)
58	Forest steppe [transect 6] (Iran)	14	0	0	38	PAKNIA & PFEIFFER (2011)
59	Central Persian desert [transect 3] (Iran)	12	0	0	33	PAKNIA & PFEIFFER (2011)
60	Central Persian desert [transect 4] (Iran)	11	0	0	43	PAKNIA & PFEIFFER (2011)
61	South Nubo-Sindian desert [transect 7] (Iran)	15	0	0	41	PAKNIA & PFEIFFER (2011)
62	South Nubo-Sindian desert [transect 8] (Iran)	14	0	0	45	PAKNIA & PFEIFFER (2011)
63	Semi-arid grassland (South-Africa)	26	0	0	28	LINDSEY & SKINNER (2001)
	TROPICAL AND SUBTROPICAL WOODLANDS					
64	Fynbos shrubland (South Africa)	45	7	43	53	DONNELLY & GILIOMEE (1985)
65	Savanna woodland (Australia)	74	8	43	49	ANDERSEN & PATEL (1994)

66	Savanna woodland (Australia)	145	12	33	24	ANDERSEN (1992)
67	Savanna woodland (Australia)	58	5	7	18	VAN INGEN & al. (2008)
68	Cerrado grassland (Brazil)	48	25	18	27	FOWLER & al. (1990)
69	Open forest (Australia)	63	8	23	21	ANDERSEN (1992)
70	Tropical dry forest (Mexico)	46	17	13	15	GOVE & al. (2005)
71	Tropical dry secondary forest (Mexico)	37	8	8	14	GOVE & al. (2005)
72	Tropical dry forest [transect 1] (Paraguay)	55	5	2	22	DELSINNE (2007)
73	Tropical dry forest [transect 1] (Paraguay)	68	7	4	14	DELSINNE (2007)
74	Tropical dry shrubland (Paraguay)	48	4	5	19	DELSINNE (2007)
	TROPICAL RAIN FORESTS					
75	Monsoon vine forest (Australia)	47	6	5	33	ANDERSEN & REICHEL (1994)
76	Vine forest of cloudy wet uplands (Australia)	17	12	18	56	VAN INGEN & al. (2008)
77	Primary rain forest (Mexico)	40	10	19	17	MACKAY & al. (1991)
78	Primary wet forest (Costa Rica) [*]	68	2	2	10	ROTH & al. (1994)
79	Wet forest (Costa Rica) #	31	3	1	33	KASPARI (1996)
80	Wet forest (Panama) #	26	0	0	33	KASPARI (1996)
81	Lowland rainforest [IFR] (Guyana)	84	0	0	35	LAPOLLA & al. (2007)
82	Lowland rainforest [MHC] (Guyana)	62	0	0	52	LAPOLLA & al. (2007)
83	Cloud rainforest [MAU] (Guyana)	40	0	0	43	LAPOLLA & al. (2007)
84	Cloud rainforest [MAF] (Guyana)	42	0	0	66	LAPOLLA & al. (2007)

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