Trophic and temporal specialization in tropical ants and its relation to species coexistence and ecosystem functioning

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Fig.1 *Leptogenys* in Borneo are capable of taking down huge crickets by their atypical swarming behaviour.

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Summary

Niche differentiation is thought to be one of the main mechanisms how species avoid competitive exclusion. However, to assess differentiation in several niches, a multifactorial approach enabling several niche dimensions to be measured simultaneously is necessary. In this way, the relative effects of several factors can be quantitatively compared in a single ecological context. Tropical ecosystems represent an especially interesting study system where invertebrates in general show high species density and diversity, and consequently high interspecific competition. This is particularly the case in ants where a few dominant species usually displace others from food resources. In view of these factors, we used a new sampling method to simultaneously assess dietary and temporal specialisation of all common ants in a community. We assessed niche position as well as niche breadth (degree of specialisation), for food and for differences between night and day in the paleotropics and neotropics in forests with differing status.

In chapter 1, we were able to show how temporal and dietary specialisation can significantly contribute to local ant coexistence.

Although ecology in the past decades has focused much attention on phenotypic plasticity, its consequences for the biodiversity-ecosystem functioning (BEF) relationship have largely been neglected. Community ecology has often tended to assume that traits of interacting species are uniform within species and do not change over short periods of time. Only recently, theory has raised the question of how phenotypic variation among individuals alters the ecological functions of a community. However, to our knowledge, little empirical data has been collected demonstrating how niche plasticity may affect functional traits.

In chapter 2, we first demonstrate that these functional traits may shift drastically between conspecifics, to the extent where their niches are closer to those of other species than to conspecifics. Secondly, numerically dominant and competitive species were those with lowest niche plasticity. Even though the two most dominant species did show temporal and dietary shifts, which may render the use of functional categories misleading. In contrast, qualitative traits of certain subordinate species did not change, but their overall niche plasticity was higher than for dominant species.

Determinants of ecosystem stability have been under intense scrutiny during the last decades. Among these, temporal asynchrony is now recognised as one important factor enhancing stability and has been thoroughly studied on large scales such as seasons or years. However, in order to evaluate the merits of functional asynchrony, it seems fundamental to investigate its role across heteroclite temporal scales in order to properly assess its explanatory power on the diversity-stability relationship.

In chapter 3, we studied circadian dynamics with multifunctional redundancy of tropical ant communities. Our goal was to determine how redundancy was influenced by circadian asynchrony in relation to species richness, numerical dominance and functional performance.

Circadian asynchrony positively influenced overall functional redundancy, but the effect sizes varied between sites and tropical regions. Interestingly, the two neotropical sites showed systematic day/night differences, with lower species richness and functional redundancy at night but overall higher increase in circadian functional redundancy than in the paleoptropics where day and night were similar. Species richness invariably had a positive effect on functional redundancy, but the effect size depended on the overall functional performance of the local ant communities and on the presence of highly performing species. Finally we demonstrated the stabilizing effect of temporal specialization in numerically dominant high performing species, and that the "sampling effect" is genuine but depended on the site or time period.

Fig.2 Certain ants forage feaces such as *Trachymyrmex* in America *Source (*Joe A. MacGown**).**

General Introduction

The ecological niche

The concept of niche is central to ecology; were it not for the fact that it has been used and defined in so various ways; the niche concept could have been considered as the backbone of ecology, much as DNA is for genetics. It therefore seems necessary to clarify the historical scientific path of the ecological niche concept.

Among the first to use the term was Grinnell (Grinnell 1917), where it was established as the "*functional role and position of an organism in its community"*. This novel definition was actually narrower then it seems, as this work focused mainly on habitat requirements and behaviours that allow a species to persist and produce offspring. It was only ten years later that Elton (Elton 1927) added that the concept of niche also depends on "*its relation to food and enemies",* supporting the notion that the niche of an animal can be defined to a large extent by its size and food habits. Basically, all organisms multiply until an element of the habitat or functional niche prevents it from doing so. These abiotic and biotic factors may be density dependent (e.g. resource depletion, predation, competition…) or density independent (e.g. temperature, humidity…) and are the main regulating factors of a population. Most theory built on these factors are based on the Lotka-Volterra competition equations that tend to deal only with populations at equilibrium for which population growth *(r)* oscillates around 0 (Lotka 1920). However, real ecological systems may often be partially unsaturated in some "niches", which in itself could allow coexistence of otherwise competitively intolerant populations, consequently maintaining population dynamics in perpetual non-equilibrium.

The 1950's saw the most advances made in this field compared to previous decades. Dice in 1952 referred to niches as a subdivision of habitat where no ecological functions were directly taken in account. Clark in 1954 concurred with the initial "ecological equivalents" concept, first brought forward by Grinnell in 1924, whereby the same functional niche can be filled by different species in different geographical regions. He distinguished two separate meanings, "habitat niche" and the "functional niche". The former corresponds to the abiotic conditions like, for instance, temperature, wind speed, salinity, etc., that a species requires for its population to persist through time. The latter (the main focus of this thesis) corresponds to the interaction a species has with its environment such as trophic functions, nutrient cycling and competition (Fig.1).

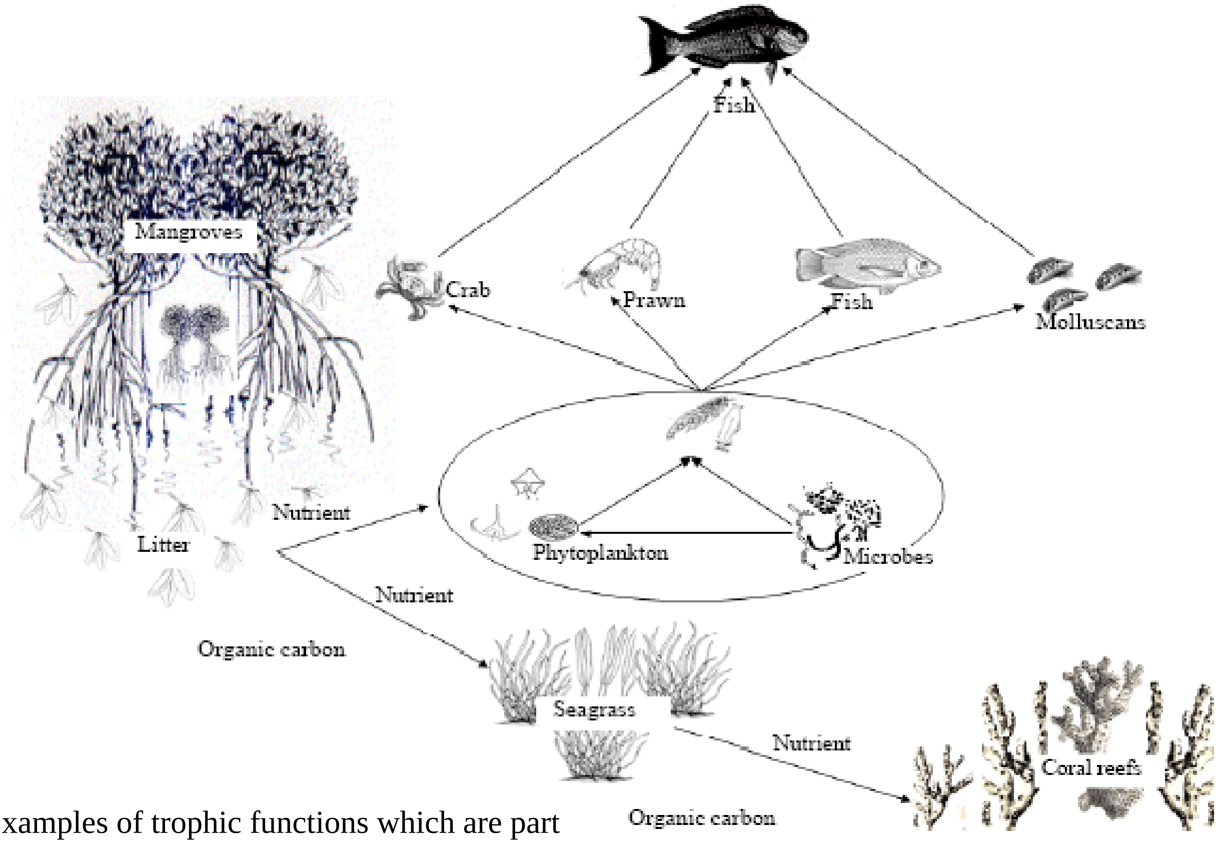

Fig.1 Examples of trophic functions which are part of functional niches (Kathiresan and Alikunhi 2011)

Species coexistence

In 1957 Hutchinson introduced the n-dimensional hyper volume niche concept, where n refers to the total range of conditions under which the individual (or population) lives and replaces itself. He introduces the fundamental and realized niche concept whereby an animal’s niche is seldom utilized to its full range of viable conditions, as Connell later demonstrated with barnacles (Connell 1961). This was an important step in underpinning possible mechanisms of coexistences between species. However, this was challenged by the “neutral theory” (Caswell 1976), which postulates that differences between members of ecologically equivalent species are “neutral” with respect to their ecological success. Stephen Hubbell’s work on the neutral theory was the most impactful (Hubbell 2001). He explained coexistence of species, on a regional (continental) scale, as a stochastic equilibrium between origination of species (speciation) and disappearance of species (extinction), and on a local scale as a stochastic equilibrium between immigration and local extinction where species have the same probability of colonizing empty sites depending on their dispersion capacity. This theory was heavily criticized which lead to a recent study (McGill et al. 2006b) which offered a general overview of the ongoing critics and found overwhelming evidence against the “neutral theory”. However, in spite of such reserves, Hubbell’s work did enable the inference of stochasticity as an important aspect of species coexistence (Andersen 2008).

The fundamental niche tends to be a hypothetical niche where no exterior forces restrict an organism, whereas the realized niche takes into account various interacting factors such as competition but also predation, parasitism and mutualism. These familiar interactions can be split into several groups, the natural enemy–victim interactions (predatory-prey, host-pathogen), the beneficial interactions (commensalism, mutualism and positive allelopathy) and competition (also negative allelopathy). Even though enemy–victim interactions are well studied interactions, competition is by far the one that has received the most attention. This is understandable in a broader ecological context, where competition concerns a vaster number of living entities, especially if intraspecific competition is taken into consideration. However, our research focuses mainly on interspecific competition in view of enlightening our understanding of species coexistence. Several different types of interactions have been demonstrated involving different interspecific competition processes from which two main categories may be established: interference competition which occurs through territoriality, and exploitative competition which occurs through resource depletion.

According to the principle of competitive exclusion, different species using the same resource cannot coexist at constant population values, if all other ecological factors remain constant (Gause 1934, Levin and Anderson 1970, May et al. 1981). In other words, coexisting species must differ in certain niche aspects, enabling them to exploit different resources (or in differing ways) or behaviourally subordinate species would become extinct. Four classes of mechanisms promoting species coexistence of potentially competing species have been suggested.

Species may coexist:

- If they experience different limiting resources at the spatial scale of the local community (resource partitioning: Turnbull, Levine, Loreau, & Hector, 2013).

- Despite the fact they experience the same limiting resources, if they are temporally or spatially separated (spatial and temporal asynchrony: Albrecht & Gotelli, 2001).
- If tradeoffs exist between competing species (discovery rate, foraging efficiency, thermal/humidity tolerance: Kneitel & Chase, 2004).
- If species adapt their ecological niche to the local community (niche plasticity: Ashton, Miller, Bowman, & Suding, 2010).

In general the conditions that promote species coexistence within communities also promote the long term stabilizing effect of biodiversity on ecosystem functioning.

Ecosystem stability

The biodiversity stability relationship (BSR) has been established over the past 60 years through the beneficial merging of community ecology and ecosystem ecology in understanding the role of biodiversity in ecosystem functioning (BEF). This relation also finds its roots in the 1950s, when renowned ecologists such as Odum (1953), MacArthur (1955) and Elton (1958) established the theoretical framework of the stability-complexity relationship (that only later shifted to the BSR). The main theoretical view put forward was that diverse ecosystems are inherently more stable than more simple ones, by implying that the more pathways there are for energy to reach a consumer the less consequential will the failure of any one pathway be, and hence the more stable the ecosystem.

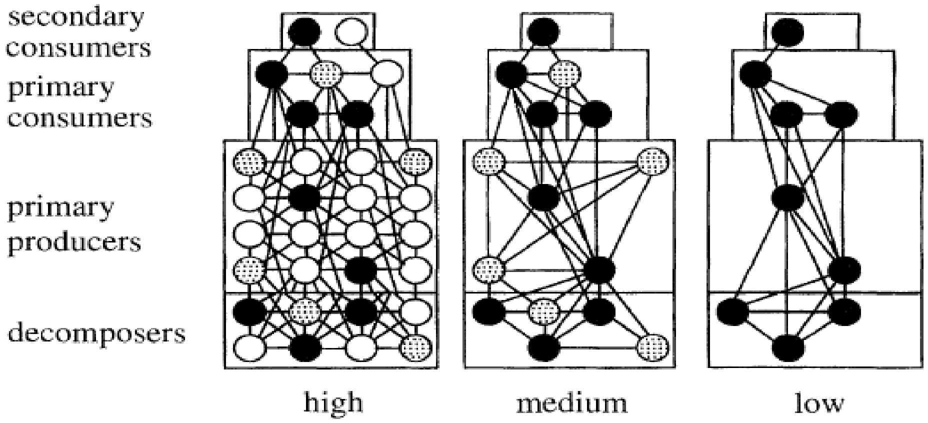

Fig.2 The relation between the complexity and stability of an ecosystem (Naeem 1995). Filled circles indicate species in all communities; grey circles indicate species only in high and medium diversity and open circles indicate species only in high diversity communities. Lines indicate biotic interactions among the species.

However, in the early 1970's this established and, by then, traditional view, was challenged by several ecologists (Levins, Garner, May and Ashby) and led to a strongly opposed theoretical view. By applying a dynamic community linearized model, in 1972 May demonstrated that the probability of stability drops abruptly after passing a certain threshold of complexity (May and Arthur 1972). One of the reasons why such opposed theoretical views were capable of prevailing, is that stability is really a metaconcept that covers a wide range of different properties as illustrated in the following Table (Loreau 2010).

Table 1. Different components of stability

Stability property	Definition
Qualitative stability	Property of a system that returns to its original state after a perturbation. Generally used for an equilibrium state.
Resilience	A measure of the speed at which a system returns to its original state.
Resistance	A measure of the ability of a system to maintain its original state in the face of an external disruptive force
Robustness	A measure of the amount of perturbation that a system can tolerate before switching to another state.
Amplification envelope	Describes how an initial perturbation from an equilibrium state is amplified within a system
Variability	A measure of the magnitude of temporal changes in a system property.
Persistence	A measure of the ability of a system to maintain itself through time.

Nevertheless, the general mechanism that generates stabilization of ecosystems properties in diverse communities is simple in principle: Different species respond differently to their biotic and abiotic environment because of differences in their fundamental niche. This consequently conveys differences in the realized niche, thus enabling the functional asynchrony of species (Loreau 2010). For example, if the populations of different species fluctuate asynchronously through time, the sum of their populations, and thereby their total functional contributions, varies less over time than that of any single species (Doak et al. 1998, Yachi and Loreau 1999, Loreau 2010, Garibaldi et al. 2011).

Temporal asynchrony can be manifested on multiple scales, e.g. as inter-annual variation, seasonal, and circadian cycles. As most work was conducted on plants, for which seasonal and inter-annual changes are most important (Isbell et al. 2011), only a few studies have investigated the role of circadian cycles for ecosystem functioning (but see Andresen 2002). Many animal taxa, however, show pronounced temporal specialisation (Fellers 1989, Albrecht and Gotelli 2001, Andresen 2002, Viljanen et al. 2010, Castillo-Rivera et al. 2011, Devoto et al. 2011, Harvey et al. 2012). Such circadian dynamics are important for ecosystem functioning. First a temporally specialised species contributes less to overall ecosystem functioning than a species active day and night. Second, if functions are taken over by different species during different time periods, the stability of the whole system increases since the functions rest on more species. Hence, these ecosystems will be more robust to extinctions of single species. Through this thesis we will investigate functional circadian asynchrony and its stabilizing effect on ecosystem functioning based on functional traits.

Functional traits

Initially species richness was used as a measure of ecosystem stability (Naeem 1995, Chapin III et al. 1997), but this research was conducted on relatively simple, species-poor assemblages. More recently, studies have shown that ecosystem functions are dependent not on the number of species itself but on the functional traits of these species (Hooper 1997). This gave rise to the emergence of the term “functional diversity” which was defined “as the value and range of functional traits of the organisms in a given ecosystem” (Tilman 2001). An increasing number of experiments were conducted on varying scales in order to further understand the role of functional diversity in relation to the BEF and BSR: from small algae cultivation (Steudel et al. 2012) to grassland monocultures (Walker et al. 1999), larger scale experiments like Biodepth in Europe (1999), long term plots like Cedar Creek in Minesota (Tilman et al. 1997) and finally the

Jena experiment which surpasses all others in terms of plot size and replication level (Roscher et al. 2005). But certain theories and results were thought biased. The "sampling effect" was brought forward as a possible bias in models that randomly picked species out of a pool to assemble communities (Tilman et al. 1997). In some experiments species were excluded but not enough time was left to enable species to overcome that loss through functional compensation (May 1974, Patten 1975). This phenomenon also called 'response diversity', describes the variation of responses to disturbance among species of a specific community (Mori et al. 2013), and can be particularly important for ecosystem renewal and restructuring, following an environmental change (Elmqvist and Folke 2003).

In parallel to functional diversity the concept of functional redundancy emerged, based on the observation that some species perform similar roles in communities and ecosystems and may, therefore, be substitutable with little impact on ecosystem processes (Walker 1992). This functional redundancy is controversial on several aspects; on the one hand it enables prioritization of conservation of "key" species in order to maintain ecosystem functions, and, on the other, it implies that some species are "expendable" (Rosenfeld 2002a). Additionally, the notion that species perform the same functions is faulty in view of the principle of limiting similarity, where exclusion should prevent the co-occurrence of species with identical niches (Gause 1934). In the past years new indexes have emerged that base functional diversity on measured traits such as abundance, biomass and spatial distribution but are mostly based on primary producers (Mason and MacGillivray 2003, Mason et al. 2005).

The higher feasibility in defining functional traits and experimenting on non-mobile organisms such as plants, and the economic benefits of further understanding functional performance for agricultural purposes, may explain why most studies until now are limited to them, and studies at higher trophic levels of functionally important organisms such as ants, are scarce (Lewis 2009). Additionally, probably because of overwhelming diversity of species in the tropics, there is still a lack of work based on these ecosystems. Yet forest clearance for intensive agriculture or timber is a major component of tropical forest degradation, with approximately 5.8 million hectares of tropical forests converted to pasture and plantation globally per year (Mayaux et al. 2005). Hence tropical ecosystems are the most vulnerable to degradation and urgently need a clear understanding of their ecosystem functions with regard to biodiversity (Lewis 2009).

Researchers have started tackling these issues and have studied the ecosystem processes in the tropics on higher trophic levels of certain invertebrates (Bihn et al. 2010, Schuldt et al. 2014). But actual functional traits still need to be measured and field data commonly include only vague proxies for very few functional parameters, where it remains unclear which of the traits are actually relevant for ecosystem functioning (Hodapp et al. 2013). This renders the use of functional diversity and response diversity crude measures for most invertebrates. Measuring accurately the stability of an ecosystem through its biodiversity still remains a crucial and problematic point in ecology.

Understanding how changing biodiversity influences the broad suite of processes that ecosystems perform is not simple. The field of biodiversity and ecosystem multifunctionality is still relatively data poor compared with explorations of biodiversity effects on single ecosystem functions. Even today our understanding of how diversity affects ecosystem functioning may be limited or even biased by the current single functional approach. It is essential to develop a mechanistic understanding of why diversity does or does not affect ecosystem on a multifunctional bases (Byrnes et al. 2014). Even if considering a maximum of parameters, it nevertheless remains expected that some species are more alike in their functional traits than others. This is where the paradigm of functional niche lies, defining similarity of species niche based on defining their functional traits (Walker 1995, Rosenfeld 2002b), knowing that discrete traits can shift two species from similar to complimentary (e.g. thermal tolerance). Therefore the level of scrutiny with which is analyzed a species traits in a community, can have direct consequences on the species functional niche, hence is subjective to the type of study. This implies that the conventional measures of functional trait diversity may mean that we are overlooking ecological important changes to communities.

In view of this, we therefore introduce a reversed approach where, instead of analyzing how many specific functional traits a given species presents, we study seven a priori defined ecosystem functions performed by tropical ants and assess each species' contribution to them.

Tropical ants

Ants are important as primary and secondary consumers in most terrestrial habitats. They represent one of the most diverse and abundant animal taxa in tropical rainforests (Hölldobler and Wilson 1990). Additionally, patterns of ant species richness and composition in degraded habitats have been shown to reflect recolonization by other invertebrate groups (Majer 1983), and are considered good soil bioindicators (Folgarait 1998). Certain ant species affect the ecosystems by moving soil (‘ecosystem engineers’) or hollowing out wood cavities (Folgarait 1998). However, due to their high biomass, probably their most important effect on ecosystem processes and nutrient cycles happens through their consumption of resources (trophic functions).

Previous studies on tropical ecosystem processes on ants (Bihn et al. 2010, Woodcock et al. 2013) represent a big step towards understanding the functions underlined in invertebrates. However, they are mostly based on indirect, unclear measures of a species’ functional relevance such as morphological traits or stable isotope signatures. For instance, relative eye size is considered to correlate with the main foraging period (diurnal or nocturnal: Bihn et al. 2010). Even though relative eye size may be a suitable measure of nocturnal versus diurnal species, this does not elucidate the morphological trait of a species active both day and night. Besides, the same trait has also been used (depending on the subfamily) in distinguishing predatory and omnivore species (Weiser and Kaspari 2006). Albeit stable isotope analysis (SIA) has proven to be a useful tool in reconstructing diets, characterizing trophic relationships, and constructing “food webs isotopes”, this method fails to account for specific dietary preferences due to multiple sources of variation in isotopic signatures (Boecklen *et al* 2011) and mostly provides information on the type of consumer (e.g. predator, herbivore). Additionally a switch of diets during a species development may cloud SIA results especially in holometabolous species such as ants.

Methodological aspect

With regard to the issues mentioned above, we thought a more direct approach through the quantification of species foraging specific resources would enable a more suitable analysis of the trophic traits of species foraging. We therefore preferred using a range of complimentary baits reflecting natural resources that could be related to trophic functions. During this thesis, we attached particular attention to the novel aspect of our methodological functions as this was the base line measure of our trophic functions.

Several studies have used baits as a focus for analysing ecological aspects of ants related to food resources (Fourcassié and Traniello 1994, McGlynn and Kirksey 2000, Lebrun 2005, Wiescher et al. 2011, Menzel et al. 2012). However two main issues arise regarding this traditional sampling technique called “cafeteria experiment”. A majority of studies have been using cards for displaying baits for monitoring (Bestelmeyer 2000, Morrison 2000, Fellers and Fellers 2012, Parr and Gibb 2012). This has little effect on the ants’ foraging behavior (Fellers 1989). However this display of the bait meant to facilitate observation limits the accuracy of identification and quantification of small morphospecies especially at night time and renders their retrieval hazardous. Other displays as Eppendorf tubes (Kaspari et al. 2008) with a narrow access may facilitate ant sampling but also defence against other species attracted. The issue here is to allow an efficient retrieval of the device with all the ants on the bait without facilitating monopolization. The compromise was found as in the following device (Fig.3) with slits on both sides.

Fig.3 The plastic box device in use

The box was placed 1 cm deep in the ground to have the openings level with the ground and were quickly retrieved by encasing in a box without side openings A small hole was made in the middle of the lid to squirt a killing solution at trap retrieval. As some ants may be more sensitive to plastic, the base of the box was covered with paper towel to facilitate their entry in the device.

Typically the baits consist of highly nutrient rich resources ranging from peanut butter, tuna and ham to even more processed foods such as cookies and hotdogs (Human and Gordon 1996, Retana and Cerdá 2000, Le Breton et al. 2006, Wriedt and Mezger 2008, Arnan et al. 2012). These baits rapidly attract dominant species (Bestelmeyer 2000) that forage for better quality resources (Kay 2004) but commonly limit the foraging successes of subordinate species (Fellers 1987, Andersen 1992). Cafeteria experiments have often been conducted by displaying a simultaneous range of bait types (Vepsäläinen and Savolainen 1990, Human and Gordon 1996, Völkl et al. 1999). If this does provide information on the preferences of species, it does not do so regarding the actual dietary range capacity of a species (in the absence of the preferred resource).

In the present research, we introduce a method to investigate niche partitioning and ant community structure in ground-dwelling forest ants. On each grid point, we presented eight types of baits (separately) which were not highly attractive, but reflected different natural resources. This reduces the monopolization of ecological dominant species and the foraging is limited to the single resource displayed.

Ants are known to be attracted to a whole range of natural resources. From the classic carbohydrates fruits/sugars, extra floral nectars to the more subtle ones such as melezitose, a trisaccharide found in trophobiont aphids, or through the starch found in seeds. Fungi is also known as source of carbohydrates indirectly foraged in *Attini* and also directly foraged with *Euprenolepis procera* that has been found eating *Pleurotus* (Witte and Maschwitz 2008). Nitrogen has been known to be one of the limiting resources in rainforest (Feldhaar et al. 2010) and is mainly found through scavenging or preying on live insects but also through coprophagy (Menzel et al. 2012). To attract predatory ants, two types of live baits were selected. One concerned a small abundant prey with no evading strategy. This would allow any predacious ant to recruit, opposed to the other type, a larger prey (grass hoppers) which could only be captured when encountered with no recruitment because it can, in theory escape, thus favoring large predatory ants (Cerdá et al. 1998). Preliminary tests were run to select the most suitable baits, each type being tested with at least four replicates. The objective was to have a complementary range of baits where ants are found recruiting and which reflect natural resources available in rainforest areas.

This resulted in the following selection: sucrose (20%; 3ml), melecitose (20%, 3ml), crushed-meal worms (4-5mg), chicken excrement (4-5mg), seed mixture (4-5mg), oleique acid (3ml) termites (small prey) and crickets (big prey). The liquid solutions were poured directly on the paper towel that served as support and the solid baits were displayed on the center of the boxes.

Baiting with live baits being something fairly scarce in ant sampling (Santamaria et al. 2009), we have detailed this particular type of baiting accordingly.

Fig.4 The 8 different baits displayed for one usual sampling session.

Concerning the larger type of prey, the advantage of grass hoppers is that no breeding was required as they are highly abundant in the required size (between 1.5 up to 2 cm) and relatively easy to sample. The difficulty lay in maintaining the cricket’s ability to jump on the one hand while, on the other, restraining it to the device. A compromise was found by tying adult grasshopper wings to a fine 5cm long string pinned to the base of the boxes, the height of the device enabling the grasshopper to still jump but not escape. Moreover this slowed down the ant’s capacities to retrieve the grasshopper which was thought to increase the likelihood of retrieving the predatory ants. A similar method was elaborated for the termites: approximately ten were maintained free and were naturally kept to the small piece of termite mound which was added while around 5 others were glued live on to a 2cm stick to avoid having all the termites being captured before the end of the sampling.

The sampling method was employed on a total off four sites in the neo and paleotropics on secondary and primary forest (Fig.5). The first two chapters on mechanisms of coexistence involve respectively the secondary forest site in French Guyana and both sites in Borneo. Only the final chapter on ecosystem stability is based on all sites. In the first chapter, with regard to the principle of limiting similarity, we look if species with similar dietary and temporal preferences co-occur less than species further apart. In the second chapter we investigate to what extent functional traits are fixed and the role of niche plasticity in the face of competition. Finally, the third chapter deals with importance of circadian asynchrony for ecosystem stability in relation to trophic performance and functional redundancy.

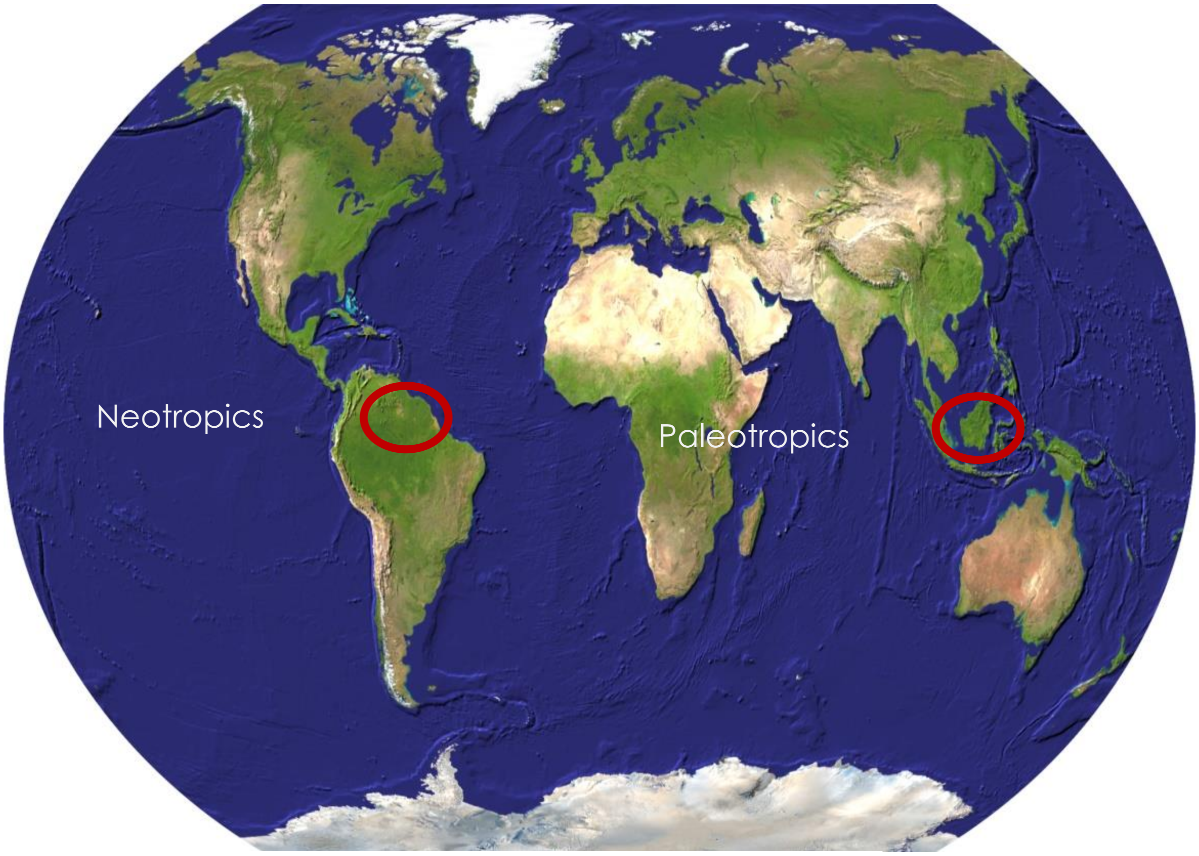

Fig.5 Location of different tropical regions studied.

This chapter is based on an original research article published in *Biotropica* in March 2015.

Chapter I: Dietary and temporal niche differentiation in tropical ants - can they explain local ant coexistence?

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Key words

Functional traits; baiting; dietary specialisation; niche breadth; partitioning; temporal distribution; ants

Abstract

How species with similar ecological requirements avoid competitive exclusion remains contentious, especially in the species-rich tropics. Niche differentiation has been proposed as a major mechanism for species coexistence. However, different niche dimensions must be studied simultaneously to assess their combined effects on diversity and composition of a community. In most terrestrial ecosystems, ants are among the most abundant and ubiquitous animals. Since they display direct, aggressive competition and often competitively displace subordinate species from resources, niche differentiation may be especially relevant among ants.

In a forest fragment in French Guiana, we studied temporal and trophic niche differentiation in a ground ant community. Various baits were presented during day and night to assess the temporal and dietary niches of the local species. They represented natural food resources such as sugars, carrion, excrements, seeds, and live prey. In addition, pitfalls provided a background measure of ant diversity. The communities attracted to the different baits significantly differed from each other, and even less attractive baits yielded additional species. We detected species specialised on living grasshoppers, sucrose, seeds or dead insects. Community differences between day and night were larger than those between baits, and many species were temporally specialised. In contrast to commonness, foraging efficiency of species was correlated to food specialisation. We conclude that many ant species occupy different temporal or dietary niches. However, for many generalised species, the dietary and temporal niche differentiation brought forward through our sampling effort, cannot alone explain their coexistence.

Introduction

Even though challenged by the neutral theory of biodiversity (Hubbell 2001), which claims that much of the diversity we observe can be explained without invoking species' differences, niche differentiation is still broadly seen as the central mechanism explaining species coexistence and diversity (Chase and Leibold 2003). Indeed, the principle of limiting similarity states that competitive exclusion should prevent the stable coexistence of species with identical niches (Gause 1934, Morrison 1996, Sanders and Gordon 2003). As a consequence, local species richness may be limited when there is little niche diversification and specialisation (Stephens and Wiens 2003). Nevertheless, in the tropics where species richness is among the highest, it is essential to understand, "how identical is 'identical'?" (May and Arthur 1972). As Agrawal and Ackerly state, community ecology should move from mere lists of community-structuring factors (such as species-specific niche traits) to a predictive framework for where, when, and how multiple factors may work, both individually and in combination, to structure communities (Agrawal and Ackerly 2007).

Competition and exclusion have been considered a 'hallmark in ant ecology' (Parr and Gibb 2010, Cerdá et al. 2013). Many ant species effectively displace others from high-quality resources through direct interference, and some species can even displace others from their territories (Hölldobler 1983). Because ants are among the most abundant animals in tropical rainforests (Hölldobler and Wilson 1990), we should expect strong competition among ant species. Thus, the high local ant diversity in the tropics awaits explanation.

Several mechanisms have been shown to enhance ant species coexistence. Firstly, stochastic factors such as nest proximity to a resource, or the distance to nests of competing species greatly affect the chances of an ant colony to discover and/or monopolise a resource. A high variation in the success rate of colony establishment can result in a patchy distribution of dominant ant colonies with multiple gaps between their territories (Andersen 2008, Andersen et al. 2013). Secondly, trade-offs should prevent dominant species from monopolising all resources. Trade-offs, i.e. negative correlations, have been reported between behavioural dominance and resource discovery (Fellers 1987), dominance and thermal vulnerability (Cerdá et al. 1998; Bestelmeyer 2000) or dominance and parasite vulnerability (Lebrun and Feener 2007).

A third mechanism is niche differentiation in one or more dimensions (Hutchinson 1959). It can be temporal (seasons: Albrecht & Gotelli 2001; time of day: Fellers 1989; Santini et al. 2007; Segev and Ziv 2012), spatial (vertical, ecologically different strata: Tanaka et al. 2010), and/or linked to diet. Ants forage on a large range of food resources (Feldhaar et al. 2010). They are important arthropod predators (Floren et al. 2002; Philpott and Armbrecht 2006), but also utilize plant saps (Davidson et al. 2003; Hunt 2003) and seeds (Carroll and Janzen 1973). Nitrogen, which is often limited in rainforests, is usually obtained from live or dead animals, but also from faeces (Menzel et al. 2012). Besides, ants engage in mutualisms with plants and plant-sucking insects (Ness et al. 2010). Certain ants occupy highly specialised food niches, such as collembola, or even fungi (Weber 1966, Carroll and Janzen 1973, Johnson et al. 2001, Santamaria et al. 2009). Thus, dietary niche differentiation is a potentially important mechanism for local species coexistence. However, apart from studies on specific species, the relative contribution of different food types to most ant diets is unknown (Bihn et al. 2010). Moreover, the question remains how niche differentiation in the trophic, temporal or other dimensions interact. To answer this, it is crucial to simultaneously consider multiple niche aspects and measure their relative importance for species coexistence.

The high species diversity in tropical forests, concomitant with a relative rarity of most species, makes it hardly possible to study every species' niche in detail. Rather, it requires a community approach where species-specific niches are assessed simultaneously. Because of the principle of limiting similarity, dietary composition and temporal specialisation are essential functional traits in defining a species' niche. In the present study, we analysed food and temporal niches of a tropical ant community, and additionally assessed spatial commonness of the participating species. We hypothesized that temporal and trophic niche breadth and optima should vary between different species, especially among locally co-occurring species. Moreover, we predicted that common species should have a broader food niche. In turn, specialised species that have a narrower food niche may compensate this by a broader temporal niche, and/or should be proportionally more efficient in finding their preferred resources than generalised species.

Materials and Methods

Study site

The study was conducted on the Campus Agronomique in Kourou, French Guiana (5°09′35″N 52°39′01″W - 5.1597°N 52.6503°W). The climate is equatorial, has a mean precipitation of 3000 mm and mean humidity of 80%-90%. The study area is a continuous 16 ha forest fragment, bordered by urban grass and surrounded by residential areas. The forest type belongs to the facies *Cesalpinaceae*, *Chrysobalanaceae*, *Lecythidaceae*, of the Coastal part of French Guiana. These types of forests are characterized by high plant diversity. All sampling took place from February to March 2012 and was performed only in absence of rain, and in dry soil to avoid any bias linked to field conditions.

Choice of baits

We aimed for a complementary range of baits which reflected natural resources available to ants in a rainforest, and used the following set of baits: sucrose (20 vol.%; 3ml; the most common disaccharide in extrafloral nectar), melezitose (20 vol.%, 3ml; a trisaccharide commonly produced by trophobionts), crushed mealworms and grasshoppers (2-3g), chicken excrement (2-3g), a seed mixture (2-3g composed of ground corn and sunflower, millet, lin, soya, barley, dari, phalaris and grass seed), oleic acid (3ml; common in both dead insects and elaiosomes), living termites and living grasshoppers. Live baits have been rarely used up to now (Santamaria et al. 2009), but they may represent an important part of an ant community's diet. We selected *Anoplotermes* termites, which do not have a soldier caste and represent a small prey without chemical or morphological defences. As a second prey type, we selected grasshoppers (Caelifera: Acrididae) representing a prey which was larger (1.5-2.5 cm), more mobile and had a harder integument than termites. Overall in terms of bait attractiveness, sucrose and crushed insects are considered most attractive as they present easy foraging and highly nutrient resources (Blüthgen and Fiedler 2004a), followed by melezitose, termites and grasshoppers, still very nutrient but harder to assimilate. Finally seeds, oleic acid and chicken excrement were assumed to be the least attractive because of low nutrient content.

Sampling design

We established four plots of 4 x 4 grid points each (16 points per square plot), i.e. a total number of 64 grid points. The grid points in the plots were separated by 10 m each; all plots were less than 100 m from one another. At each grid point, we presented in total eight different baits, both during day and at night, and placed pitfalls during day and at night. However, to avoid interference between multiple baits, only one bait or one pitfall was presented at each grid point at a given time. We took care that, during each sampling session, all eight baits were presented evenly (at different grid points), in order to avoid any bias due to fluctuating weather conditions. Pitfalls were only placed when no baiting was performed on the same plot.

All ants collected were preserved in 75% ethanol. They were counted and sorted to morphospecies by Mickal Houadria and Alex Salas-Lopez, based on Bolton (1997). Voucher specimens of all species are deposited at the Institute of Zoology, University of Mainz.

Pitfalls

The pitfall traps (Ø 4cm, depth 6cm) were buried in level with the surrounding soil surface and replaced after each sampling session (into the same hole) to reduce the digging-in effect (Greenslade 1973). They were opened for 10 hours between 20h30 to 6h30 for the nocturnal traps and between 7h00 to 17h00 for the diurnal ones. For each grid point, we obtained three 10-hour replicates day and night, yielding a total of 60 sampling hours. To kill and preserve the ants, the traps were filled ca. 1.5 cm high with a 50% propylene glycol solution. This preservative is non-toxic to vertebrates at these quantities and neither attracts nor repels ants (Boonzaaier et al. 2007).

Displaying the bait

Many studies use some sort of card to expose baits (Pearce-Duvet et al. 2011, Gibb and Parr 2013). This has little effect on the ants' foraging behaviour (Fellers 1989), but makes it difficult to retrieve them. Narrow access to baits, in contrast, facilitates ant sampling, but hinders recruitment and possibly promotes bait monopolisation of one ant species against others. Therefore, we presented baits in circular plastic boxes with lids. Access to the bait was maintained as wide as possible to hamper bait monopolisation. The boxes were placed 1 cm deep in the ground and had, 6 mm above the bottom, two slit-like openings (1 cm wide and 8 cm long), level with the ground. They could be quickly retrieved by encasing into a similar box without side openings. As plastic is potentially avoided by some ants, the base of the box were covered with paper towel. A hole in the lid allowed squirting the killing solution (propylene glycol solution 70%) right after retrieval.

The liquid solutions were pipetted directly onto the paper towel in the baiting device while the solid baits were put into the centre of the devices. Live baits were harder to display. Approximately ten termites were maintained free on the paper towel and usually stayed at a small piece of termite mound which was added. To avoid that all termites would be captured before the end of the sampling approximately five further individuals were glued live on a 2 cm stick with odourless rat glue (Greenleaf Ltd., Beijing, China). For grasshoppers, in order to partly maintain their ability to jump but restrain it to the baiting device, we tethered it to a fine, 3 cm long string which was pinned to the base of the boxes.

The baits were presented for 90min during the day (between 10h00 and 15h00) and at night (between 20h00 and 23h00). Preliminary tests had shown that this time was sufficient to allow at least partial recruitment on all baits, but was not long enough to have dominant ants saturating the majority of the most attractive baits.

Data analysis

In our analyses, we used frequency and incidence data. 'Frequency' is defined here as the number of occurrences, i.e. the number of times an ant species occurred at baits (regardless of the actual number of individuals). 'Incidence', in contrast, denotes the spatial commonness, i.e. the number of grid points (out of 64) where a species was captured at all. For example, a species caught at two different baits at the same grid point will have a frequency of two, but an incidence of one.

Comparison of sampling methods and baiting efficiency

Exhaustiveness of the different sampling methods (eight bait types, total baits, and pitfalls) was estimated by calculating Cole's rarefaction curves. Furthermore, we estimated the expected species richness with the Chao2 species richness estimator, using EstimateS 8.20 (Colwell 2013). The respective data were pooled according to the 64 grid points. For the eight bait types, each data point (grid point) thus represents two baits (day and night, 2x90min); for total baits, it is 16 baits of 90 min each, and for the pitfall samples each data point represents six nocturnal and diurnal pitfall replicates (6 x 10 hours). Comparison between the ant communities sampled with baits and pitfalls was calculated using Bray-Curtis method where the relative abundances of the species on each sampling technique was standardised.

The ant communities at different baits and times of day (based on presence absence) were analysed using PERMANOVA (Clarke and Gorley 2006), with 'bait type' and 'time of day' as fixed factors and 'grid point' as random factor; furthermore, we tested for day/night differences for each bait type separately using PERMANOVA. Similar analyses were conducted to test for temporal differences on ant communities sampled with pitfalls. Further analysis was conducted with PERMANOVA for grid-point-wise presence/absence data to compare pitfall and bait data, with 'time of day' and 'capturing method' as fixed and 'grid point' as random factors.

Food specialisation

Food specialisation was assessed based on Simpson's diversity index. Incidence was chosen over frequency to be sure that all the food choices were not from only one or two grid points, which could limit the species capacity in foraging several times the preferred resource. We chose 10 as a cut-off value for there to be a clear possibility for the species to have gone to the other seven resources. For each species *n* (with a frequency ≥ 10), we calculated its total frequency on each bait, and calculated its food specialisation as $fs_n = \sum p_i{}^2$, where p_i is the frequency of ant *n* on bait *i* divided by its total frequency.. A common species, however, is more likely to encounter different baits just by chance. Therefore, we calculated fs_n for each species 1000 times, each time based on a total frequency of species *n* rarefied to 10 occurrences.

Food preferences and foraging ratio

As used here, 'food specialisation' looks at the relative exclusiveness of a species for any resource (i.e. a measure between 0 and 1), whereas 'food preferences' provide information if, and which, resources are significantly preferred. A species specialised in one resource will prefer it, but a species with one or several preferences may or may not be highly specialised overall (Fig. 4). For each species, we conducted 1000 permutations per species to assess on which bait the incidence was higher than expected from random (preferred bait). This was done by randomly assigning the summed incidences per bait to the five different baits; we then calculated the quantile of the real value against these null distributions, and deemed them significant if they fell outside the 95% confidence interval.

The foraging ratio (*fr*) of a species was calculated as the ratio of a species' frequency on its most preferred bait (highest frequency) divided by its overall frequency in pitfalls. A high foraging ratio implies that few scout ants (as measured by pitfall frequency) suffice to efficiently find baits, i.e. they suffice for a relatively high frequency on their favoured bait.

Temporal niche and specialisation

For each species *n* with a frequency ≥ 10, we calculated its temporal niche tn_n by comparing its total frequency during day and at night. tn_n was calculated as

$$tn_n = 2 \cdot \frac{fr_{day_n}}{fr_{day_n} + fr_{night_n}} - 1$$

Where tn_n is the temporal niche position, $fr_{day,n}$ and $fr_{night,n}$ are the total number of occurrences during day and night, respectively *tn* ranges from -1 (purely nocturnal) to +1 (purely diurnal). This metric was calculated twice for each species, once based on pitfall frequencies and once based on bait frequencies. We interpret the pitfall-based *tn* as a measure of the ant's foraging activity (when the ants is actively scouting for food resources). In contrast, the bait-based *tn* measures when the ant actually succeeds in foraging and recruiting. Significance of a species' temporal specialisation was assessed with a paired Wilcoxon test for grid point-wise frequency at night and during day. Temporal specialisation was calculated as $ts = |tn|$, and ranges from 0 (no specialisation) to 1 (purely nocturnal or purely diurnal). Wilcoxon signed-ranks test was used for evaluating if a species temporal distribution significantly diverged from no specialisation, i.e if it was significantly more present at day or night. Correlations between different functional traits (*tn, fs, fr*) were done using Spearman rank correlations.

Niche differentiation and co-occurrence

Finally, we assessed the impact of temporal and trophic niche differentiation on co-occurrence. For each pair of species, we calculated the 'absolute co-occurrence' as the number of grid points where both species had been found. We constrained this analysis to the 13 most common species, such that we included all species that co-occurred at least 10 times, since rarely co-occurring species would not require niche differentiation. 'Relative co-occurrence' was calculated by absolute co-occurrence divided by the average incidence of both species. Temporal niche differentiation was obtained as the difference between *tn* values; and dietary niche differences was calculated as the Bray-Curtis distance between the incidences of the two species on each of the eight baits. If niche differentiation explained co-occurrence, then locally co-occurring species should have higher niche differences than species that did not co-occur. We used a partial Mantel test (command *mantel.partial*) to analyse the correlation of absolute or relative co-occurrence with temporal and trophic niche distance. All analyses (if not mentioned otherwise) were conducted using R version 2.15.2 (R Development Core Team 2012).

Results

Table 1: Total abundances, occurrences, and total species richness at each bait, and totals for diurnal and nocturnal baits. Estimated species richness is given as the mean of Chao2 estimator values. *For baits with high variation in abundance, the uncorrected Chao1 estimator was higher than Chao2, and therefore used as recommended by Anne Chao.

bait type	abundance	occurrences	total species richness	estimated richness
Sucrose	6403	218	23	25.95
Melezitose	4365	188	23	32*
Crushed insects	2382	162	25	38.78
Grasshoppers	1900	97	19	19.49
Oleic acid	1371	90	16	32*
Seeds	651	95	22	47*
Termites	321	92	19	21.95
Chicken faeces	170	60	18	21*
Day	9635	517	32	-
Night	7906	485	25	-

Ant communities in baits and pitfalls

A total of 34 species were captured on baits and 47 in pitfalls. This yielded a total of 52 species (including 10 singletons), with 29 species captured both with baits and pitfalls. Species richness at the site was estimated as 38 species (mean Chao2 estimate; range: 35-56) captured with all baits, while 52 species could have been sampled with pitfalls (range: 48-67) (Table 1, Fig. 1). Thus, mean species estimates were close to the actual numbers we captured with all baits pooled and with pitfalls. Ant communities on baits and pitfalls were significantly different (PERMANOVA with presence/absence data: pseudo-F = 18.9, df = 1, p = 0.001), both overall and when analysed separately for day and night data (each $p \leq 0.001$). Bray Curtis distance of ant assemblages between pooled baits and pitfalls was 0.717 (standardised abundance).

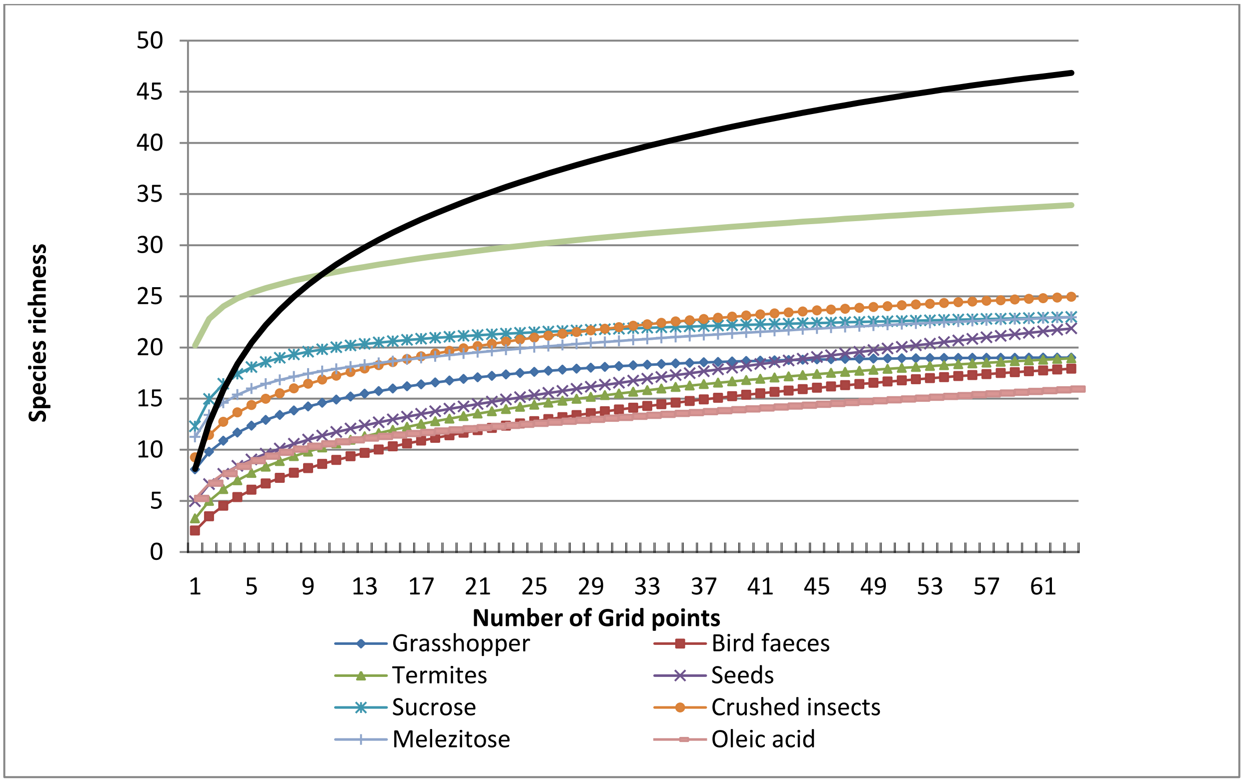

Fig. 1 Rarefaction curves for the eight bait types, for pitfalls and all baits pooled. In each case, samples were pooled according to grid point, such that each rarefaction curve is based on 64 samples.

In total, 21 species were caught on at least 10 grid points using baits or pitfalls (Table 2). Ten of these were much more often caught at baits. Their incidences at baits were more than twice the incidences on pitfalls, while the opposite was only true for two species (Fig. 2). After correction for the total incidences on baits and in pitfalls, three species were caught significantly more often on baits (*Camponotus* sp. 2, *Crematogaster limata*, *Pheidole zeteki*), and three species in pitfalls (*Pachycondyla crassinoda*, *Sericomyrmex* sp. 1, *Trachymyrmex* sp. 1) (χ^2 tests: all $\chi^2 > 5.6$; $p \leq 0.018$).

Table 2. The more common species (total incidence ≥ 4) with abundance, incidence, food and temporal specialisation. *fs*: food specialisation based on unrarefied frequency data. Significant food preferences were determined with randomization tests; the temporal niche was tested against an equal day-night distribution using chi^2 tests. ‘Gra’: live grasshoppers; ‘Cru’: crushed insects; ‘See’: seeds; ‘Suc’: sucrose. 'n/a': Frequencies too low (<10) for analysis. 'ns': not significant. Significant food preference, and significant temporal niches (i.e. different from an equal day-night distribution) are denoted with asterisks (*p < 0.05; **p < 0.01; ***p < 0.001). Significant differences between temporal niche from pitfalls and from baits (according to chi^2 test) are denoted with superscripts. ^{1}p < 0.05; ^{2}p < 0.01; ^{3}p < 0.001. ‘ns’: not significant; ‘n/a’: too few data for estimation.

Species	abbreviation	total abundance at baits	incidence at all baits	incidence at pitfalls	Food specialisation		Temporal specialisation	
					fs	preferred baits	temporal niche pitfall	temporal niche bait
Anochetus diegensis	*Ano1*	0	0	5	n/a	n/a	n/a	n/a
Atta cephalotes	*Att1*	0	0	5	n/a	n/a	n/a	n/a
Camponotus sp.1	*Cam1*	75	11	2	0.58	Cru ***	n/a	ns
Camponotus sp.2	*Cam2*	962	51	17	0.34	Suc ***	ns^3	night***^{3}
Camponotus sp.3	*Cam3*	93	12	4	0.44	Cru ***	ns^1	night***^{1}
Crematogaster limata	*Crem1*	702	14	2	0.42	Cru ***	n/a	ns
Crematogaster levior complex	*Crem2*	556	10	11	0.28	ns	ns	day**
Cyphomyrmex minutus	*Cyp1*	1	1	4	n/a	n/a	n/a	n/a
Diplorhoptrum sp.1	*Dip1*	157	33	15	0.31	ns	day**^{1}	ns^1
Diplorhoptrum sp.2	*Dip2*	199	26	9	0.29	ns	ns	ns
Labidus sp.1	*Lab1*	0	0	4	n/a	n/a	n/a	n/a
Nylanderia sp.1	*Nyl1*	474	23	8	0.58	Suc ***	ns	ns
Odontomachus haematodus	*Odo1*	33	19	17	0.34	Gra **	ns	ns
Pachycondyla crassinoda	*Pac1*	6	3	29	n/a	n/a	ns	n/a
Paratrechina sp.1	*Par1*	150	6	1	n/a	ns	n/a	ns
Pheidole sp.1	*Phe1*	758	16	10	0.31	ns	day**	day*
Pheidole zeteki	*Phe10*	199	25	6	0.42	Suc **	ns	day***
Pheidole pugnax	*Phe11*	3294	40	33	0.33	Suc **	ns	day*
Pheidole sp.12	*Phe12*	73	15	7	n/a	ns	ns	ns
Pheidole cf. *texticeps*	*Phe16*	235	15	12	0.41	ns	day**	ns
Pheidole sp.17	*Phe17*	61	3	4	n/a	ns	n/a	n/a
Pheidole sp.18	*Phe18*	24	5	2	n/a	n/a	n/a	n/a
Pheidole sp.21	*Phe21*	60	10	7	0.32	ns	ns	day*
Pheidole subarmata	*Phe3*	5234	45	38	0.27	Suc *	ns	ns
Pheidole aripoensis	*Phe5*	249	14	14	0.32	ns	day**^{2}	ns^2
Sericomyrmex sp.1	*Ser1*	83	5	24	n/a	ns	ns	ns
Solenopsis sp.1	*Sol1*	3354	18	13	0.27	ns	ns	ns
Trachymyrmex sp.1	*Tra1*	22	10	19	0.53	See ***	ns	night*

Ant communities at different baits

The baits varied strongly in the number of individuals and occurrences but less so in total number of species attracted. The most attractive bait in terms of individuals (sucrose) attracted 37.7 times more individuals than the least attractive one (chicken faeces). However, the total number of attracted species on sucrose and chicken faeces was 23 vs. 18, respectively (Table 1). The highest number of species (25) was found on crushed insects (Table 1). Although oleic acid, chicken faeces and seeds were less attractive (as measured in number of occurrences), they attracted additional species not present at other baits. Chao's species estimations and rarefaction suggested that baiting was rather exhaustive for sucrose, grasshoppers, termites, and chicken faeces, whereas more species could have been captured with further baiting of melezitose, crushed insects, seeds, and oleic acid (Table 1, Fig.1).

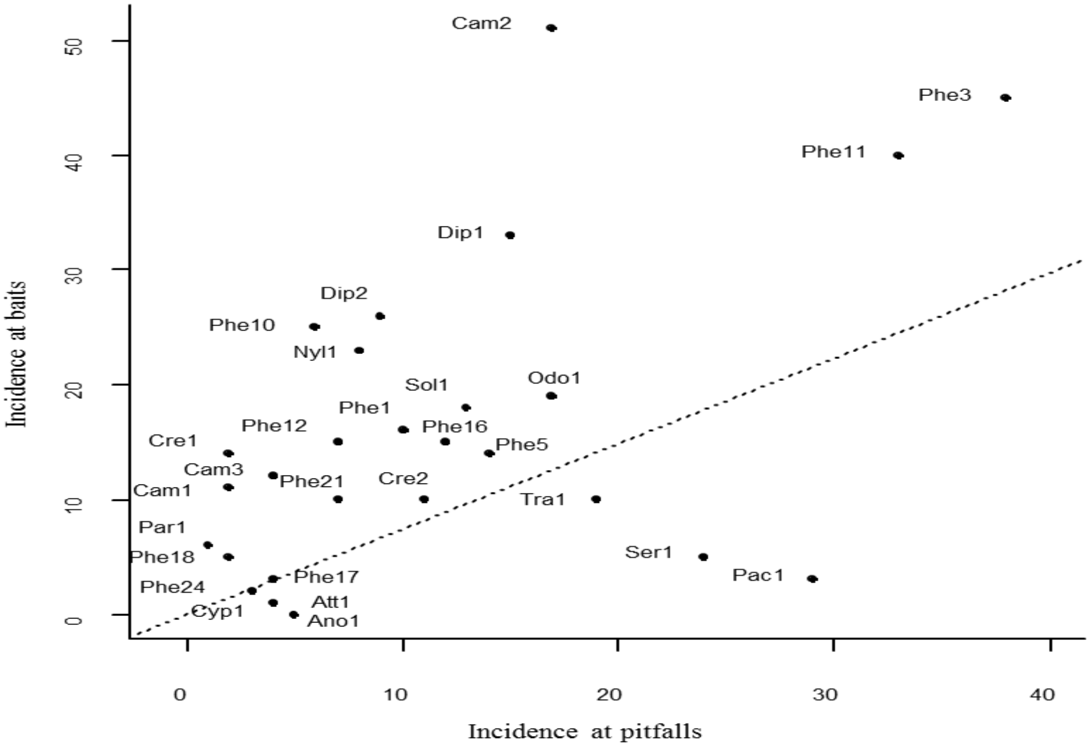

Fig. 2 The slope of the dotted line equals the ratio of the summed incidences at baits and in pitfalls, to correct for different capture rate of baits and pitfalls. Species abbreviations are given in Table 2.

Species composition on the different baits differed greatly (PERMANOVA on presence/absence data: pseudo-F = 9.5; df = 7; p = 0.001); but the differentiation between day and night was even higher (pseudo-F = 25.8; df = 1; p = 0.001) (Fig. 3). The interaction between bait type and time of day was significant (pseudo-F = 2.9; df = 7; p = 0.001)**.** When ant assemblages were analysed for each bait type separately, we found significant temporal differentiation for seven bait types (each $p \leq 0.016$) but not for oleic acid (p = 0.062). Ant assemblages in pitfalls were also significantly different between day and night (pseudo-F = 5.9; df = 1; p = 0.001). Ant assemblages on melezitose and sucrose (PERMANOVA: p = 0.061) did not differ significantly in pair-wise presence/absence comparisons, nor did those recorded on termites and grasshoppers (PERMANOVA: p = 0.625) or those between oleic acid and seeds (PERMANOVA: p = 0.085). Consequently, melezitose, termites and oleic acid were omitted from the analysis of food specialisation, and only sucrose, grasshoppers, and seeds were retained, for yielding more occurrences (Table 1). Pooling similar baits would have resulted in unequal sample numbers and thus biased further analysis. All other baits significantly differed from one another in the ant communities they attracted, even after correction for false discovery rate (Benjamini and Hochberg 1995) (all $p < 0.05$).

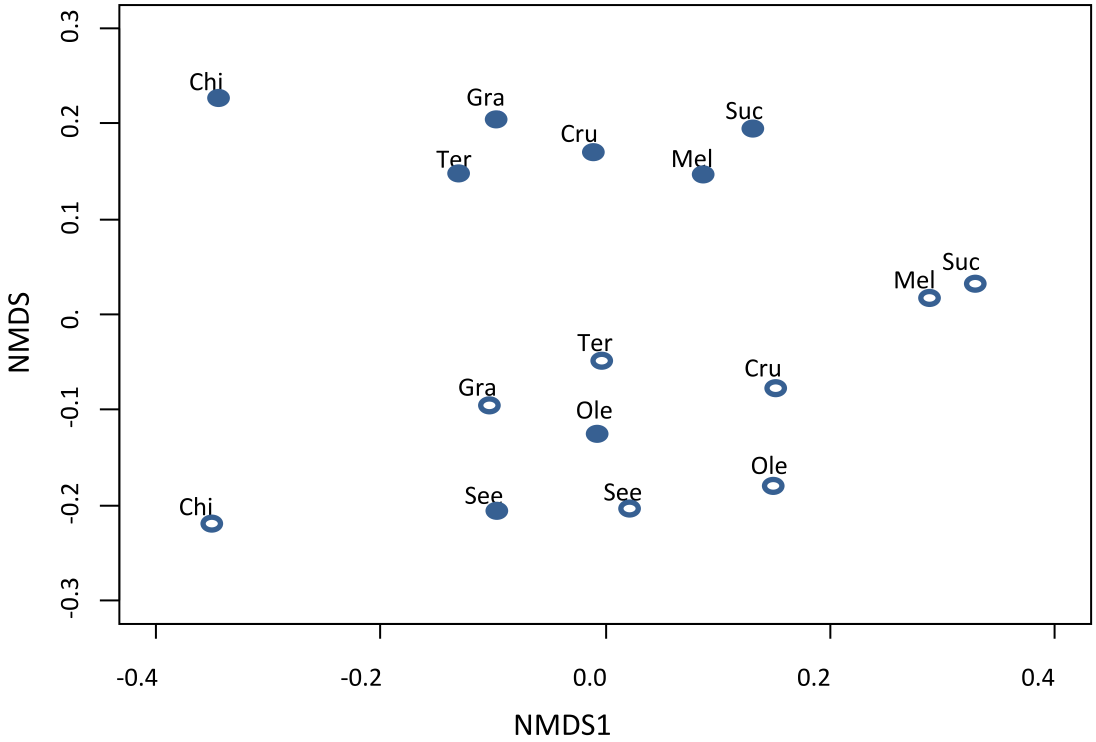

Fig. 3 NMDS ordination, based on presence/absence data, for the ant assemblages attracted to the eight food baits and the two time periods. *Cru*: crushed insects; *See*: seeds; *Suc*: sucrose; *Mel*: melezitose; *Gra*: live grasshoppers; *Ter*: live termites; *Chi*: chicken faeces; *Ole*: oleic acid. Full circles represent nocturnal and empty circles diurnal baits.

Food specialisation and preferences

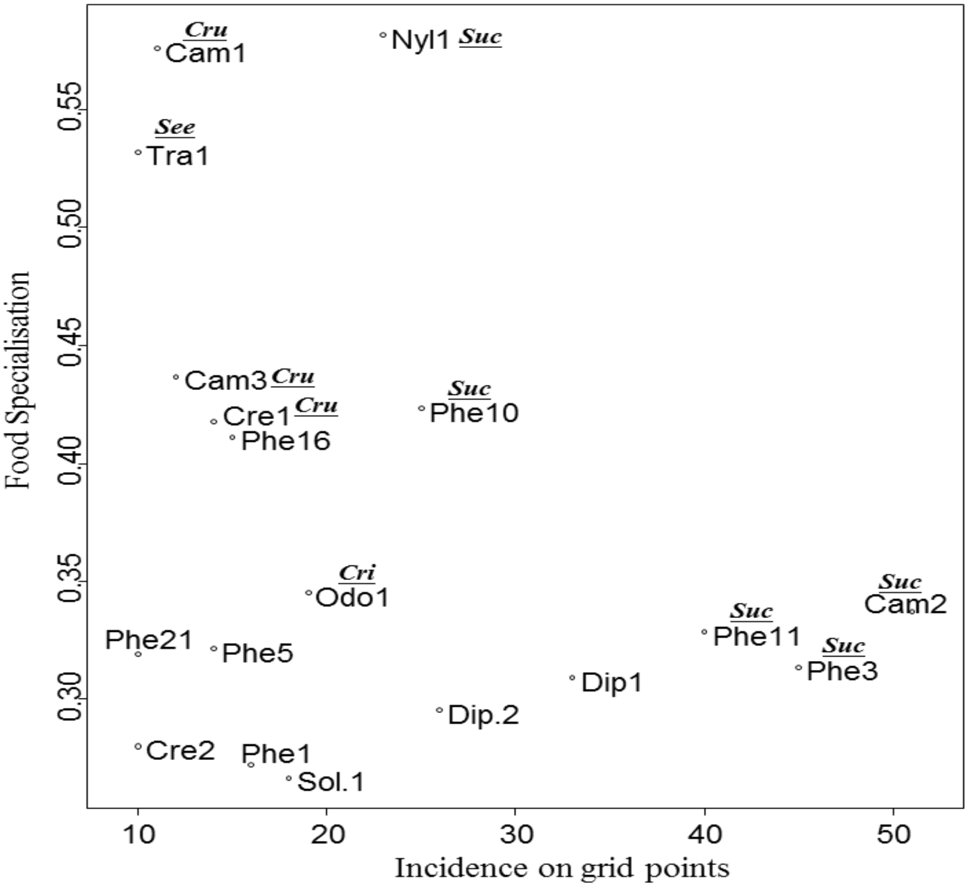

Fig. 4 Rarefied food specialisation *fs* plotted against incidence at baits. This index can range from $fs_n = 5* (1/5)^2 = 0.2$ if all five bait types are used equally (with each $p_i = 1/5$), to $fs_n = 1.0$ in the case that only a single bait type is used. For species with significant food preferences, the preferred baits are given: *Cru* (crushed insects), *Gra* (grasshopper), *Suc* (sucrose), *See* (seeds). Species abbreviations are given in Table 2.

We calculated *fs* for 18 species with an incidence ≥ 10 at the five baits (omitting the baits melezitose, termites and oleic acid). Our results showed that no species were fully specialised or absolute omnivores, instead, that a full gradient of species with varying dietary habits existed.

Among the 18 species we analysed, only ten showed significant food preferences (Fig. 4, Table 2). Five species, including the three most abundant ones, significantly preferred sucrose over the other baits. *Camponotus* sp.1 and 3, and *Crematogaster limata* preferred crushed insects. In contrast, among the eight *Pheidole* species, none preferred crushed insects, but three of them (*Pheidole subarmata*, *Ph. zeteki* and *Ph. pugnax*) had a preference for sucrose. *Odontomachus haematodus* was found to prefer grass hoppers than other resources, and *Trachymyrmex* sp.1 preferred seeds.

Temporal specialisation

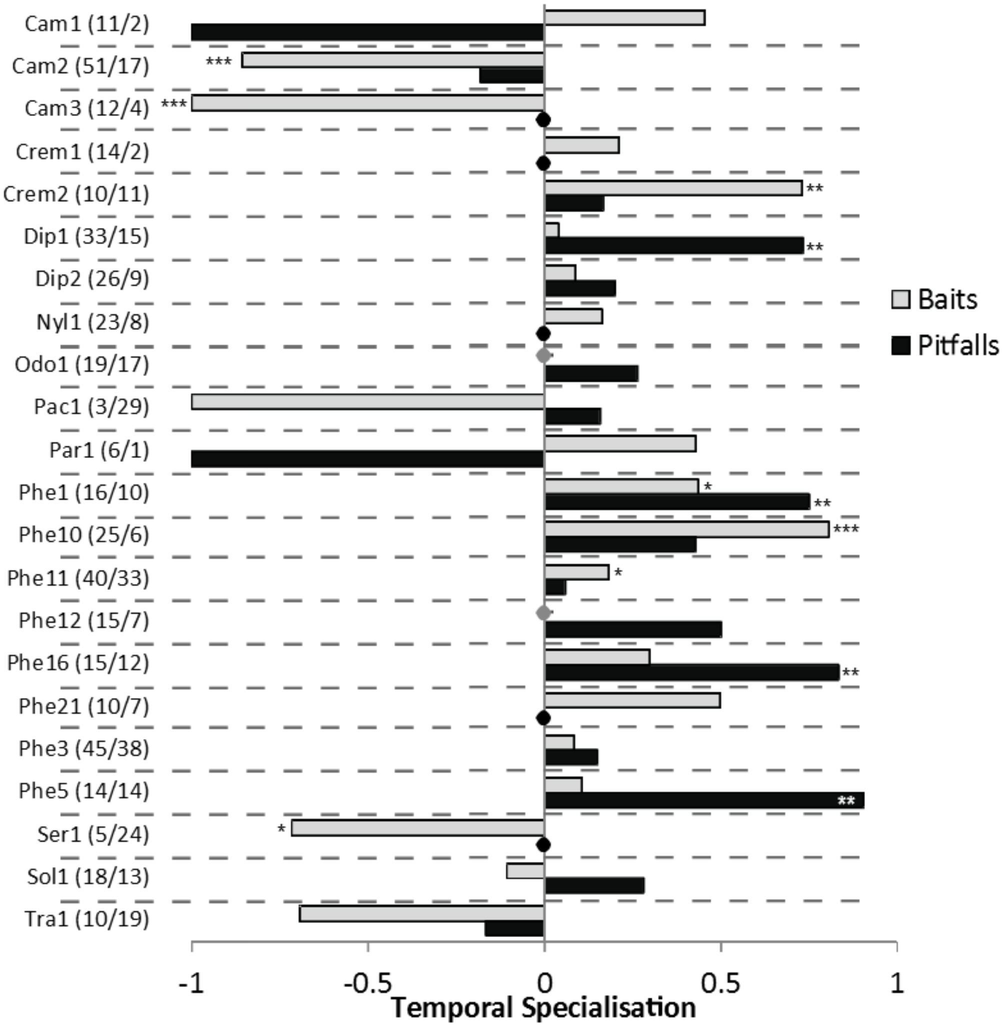

Fig. 5 Temporal specialization at baits and in pitfalls, based on species frequencies. Significant temporal specialization (according to χ^2 test) is indicated with asterisks: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$. Full circles indicate a temporal niche of zero. The numbers in brackets give the incidences at baits and in pitfalls, respectively.

Overall, nocturnal and diurnal ant communities differed markedly (Fig. 3), and this effect was consistent for pitfalls and baits. Total species richness at night was slightly lower (Table 1). At baits, 32 species were captured during the day and 25 at night (total species number: 34). In the pitfalls, we obtained 43 species during the day and 31 at night (total species number: 47). The species only captured at night were two *Pachycondyla* and two *Camponotus* species, and several singletons. All other species were found both at day and night although not always evenly.

One-fourth to one-third of the species showed significant temporal specialisation (4 out of 19 in pitfalls; 8 out of 21 at baits) (Fig. 5). In the pitfalls, four species were frequently more sampled during the day, but no species were primarily nocturnal. At baits, we found three significantly nocturnal and five diurnal species. Interestingly, four species showed a significant difference in their day/night distribution between pitfalls and baits (Fig. 5; Table 2): from pitfalls to baits, two shifted from no specialisation to night (*Camponotus* sp. 1 and 2), and two shifted from day specialisation to no specialisation (*Diplorhoptrum* sp. 1; *Pheidole* sp. 5). Only one species (*Pheidole* sp.1) was significantly more abundant during the day in both baits and pitfalls.

Combining functional traits and commonness

Overall, the degree of food specialisation was not related to commonness. The food specialisation index was not correlated to incidence at baits (Spearman's rho= -0.28, p = 0.26; Fig. 4). However, although three common species significantly preferred baits, there were no species with an *fs* value > 0.35 *and* an incidence above 25. Note that two species common in pitfalls (*Pachycondyla* sp. 1 and *Sericomyrmex* sp. 1) were too rare on baits to adequately estimate their food niche. Similarly, the degree of temporal specialisation did not correlate to incidence (for baits: Spearman's rho = -0.32, p = 0.19; pitfalls: rho = -0.07, p = 0.78). Temporal and food specialisation were not correlated (Spearman rank correlation; temporal specialisation at baits vs. *fs*: rho = 0.021, p = 0.93; temporal specialisation at pitfalls vs. *fs*: rho = -0.46; p = 0.052). The two species with highest *fs* (Fig. 4) showed no temporal preferences for baits or for pitfalls. Finally, *fs* was positively correlated to the foraging ratio *fr* (Spearman's rho = 0.65, p = 0.0037), implying that specialised species had a lower incidence in pitfalls compared to their incidence at baits than generalised species.

Local co-occurrence could not be explained by niche differences. For co-occurring pairs of species, the absolute or relative number of grid point-wise co-occurrences was not correlated to the temporal or trophic niche differences (absolute co-occurrences: partial Mantel test: r = -0.089; p = 0.69; relative co-occurrences: r = -0.043; p = 0.62).

Discussion

Temporal and trophic niche differentiation in ant communities

The aim of this study was to simultaneously assess trophic and temporal niches of an ant community and investigate whether these functional traits explain ant coexistence. Both niche dimensions were found to influence community composition. Ant communities differed between bait types for five of our eight baits (sucrose, living grasshoppers, chicken faeces, seeds, and dead insects), the ant communities varied significantly for each pair-wise comparison. However, the difference between diurnal and nocturnal communities was greater than that between communities at different bait types (Fig. 3). Temporal segregation hence seems to facilitate species coexistence more than the limited range of food resources our baits represented. The significant interaction between time and food type was probably related to oleic acid, which was the only resource to not differ between diurnal and nocturnal ant communities. This may be due to *Camponotus* sp. 2, which was frequent on most baits but never foraged on oleic acid. Being nocturnal and numerically dominant, this species therefore had consequences on the temporal segregation of this resource. This result matches a study on temperate ant communities, where day/night segregation among species was high and represented an important coexistence mechanism (Stuble et al. 2011, 2013). Temporal niche partitioning of dominant and subordinate ants has also been shown in Mediterranean ant communities (Santini et al. 2007, Segev and Ziv 2012) but in most cases it is difficult to show that this is an effect of competition (Andersen 1992).

The high temporal differentiation found on community level was also detectable on species level. One-third of the ant species showed temporal specialisation in pitfalls or baits. Notably, temporal segregation was high between two of the three most common species, with *Camponotus* sp. 2 being nocturnal and *Pheidole pugnax* being diurnal. This concurs with previous findings on competition between dominant species which can regulate their distribution and temporal partitioning (Andersen and Patel 1994). Two results about species-level temporal niches were unexpected: Firstly, there were more exclusively diurnal than nocturnal species, both in the pitfall and the bait samples, although one could expect a similar number of nocturnal species which avoid diurnal competitors. The pattern coincides with a slightly higher overall abundance and frequency of ants during the day, but this cannot fully explain the rarity of nocturnal specialists. Secondly, temporal specialisation in pitfalls and baits often differed. Temporal specialisation that remained the same in both sampling methods was only found for one species (*Pheidole* sp. 1). One explanation may be that pitfalls mostly capture scouts, i.e. individuals that forage on their own. Since no food resources are involved, there should be little effects of interspecific competition on the temporal niche in pitfalls. In contrast, baits reflect the ability of species to recruit to a resource and potentially withstand competing species. We therefore tentatively interpret the temporal niche at pitfalls as unaffected by competition, whereas the temporal bait niche could be influenced by competitors. Notably, from pitfalls to baits, the temporal niche either shifted from 'diurnal' to 'unspecialised', or from 'unspecialised' to 'nocturnal', but not towards diurnal. Thus, it seems possible that some species manage to evade competitors by recruiting more heavily at night. In order to clarify these temporal shifts, in addition sampling should be performed at crepuscular times, where ant communities could differ from both day and night.

Beside temporal differentiation, communities differed between different food resources. Food resources varied greatly in their attractiveness, but even less attractive items yielded additional species. Five of the eight baits attracted ant communities that differed significantly from one another. For example, living termites and grasshoppers were much less attractive than insect carcasses, but attracted a significantly different community, including a species that significantly preferred live grasshoppers to dead insects (*O. haematodus*). This emphasizes the need to include live baits in further studies, especially since they have been scarcely used up to now (Santamaria et al. 2009), and the consumption of living or dead matter cannot be distinguished by studies based on stable isotopes. Such a differentiation, and the fact that all baits together attracted more species than any single bait type (Fig. 1), shows that there is trophic niche differentiation on community level. On species level, this was reflected in species that preferred certain food items to others. For four bait types (grasshoppers, crushed insects, sucrose, and seeds), species showed significant preferences. Remarkably, the three most numerically dominant species with highest frequency and incidence (Fig. 2 and 4), significantly preferred sucrose over crushed insects. This concords with the fact that carbohydrates and proteins meet different colony needs and that colonies spend more time foraging their limiting nutrient (Kay 2002) from which we can extrapolate that numerically dominant species may have a greater need for carbohydrates and may show 'high tempo foraging' (Davidson 1997).

Interestingly, ant communities at sucrose (a disaccharide) did not differ from those at melezitose, which is a trisaccharide common in honeydew (Völkl et al. 1999). This suggests that all species in our study that use sucrose are also able to digest melezitose. Hence, the regular consumption of melezitose-containing honeydew may not represent an option to evade competition by sucrose-foraging species. In other, mostly arboreal ant communities, however, several ant species avoid feeding on melezitose and are thus unable to effectively utilize some of the honeydew sources (Blüthgen and Fiedler 2004b). Furthermore, we had expected to find different predatory ant species at grasshoppers and termites. Apparently, the same ant species could overwhelm the two prey items regardless of their size.

None of the species preferred oleic acid, only omnivore species (mostly *Pheidole*) capable of consuming pure lipids were attracted. We had not expected this since elaiosomes are assumed to contain oleic acid as attractant (Boulay et al. 2005, Bronstein et al. 2006), but see (Reifenrath et al. 2012), and the presence of a chemical food cue alone often suffices to attract specialised species (Schmitt et al. 2004). However, no information could be obtained on the diversity of elaiosome-bearing plants at the site.

To assess food niche differentiation in ants, most studies to date applied one of the two approaches: multiple artificial baits (Le Breton et al. 2006, Cerdá et al. 2011, Arnan et al. 2012) or stable isotope analyses (Bihn et al. 2010). Artificial, highly attractive baits such as tuna or honey have often been used as a rough guide to a species' preference between carbohydrates or proteins. Our data confirmed (Table 2) that several species preferred either carbohydrates or proteins (Cerdá et al. 1989), but in many species, the food specialisation was more gradual than a crude classification would suggest (Fig. 4). Stable isotopes are a useful tool to assess the trophic position of an ant and allow to gather data for whole ant communities (Blüthgen et al. 2003), but do not allow discrimination between dietary items of the same trophic level (that is, with a similar ^{15}N signature). Stable isotope studies therefore often classify species with intermediate signature or with high intraspecific variation as omnivorous (Pfeiffer et al. 2013) but it is hardly possible to further distinguish among such species.

Despite high differentiation on community level, and the detection of species that were trophically or temporally specialised, local ant co-occurrence could not be explained by niche differences alone (as shown by partial Mantel tests). Hence, it seems likely that a finer resolution is needed to determine the niches of species that occur at the same grid points. This may include specialisation on further food items, a finer temporal differentiation, or differing seasonal foraging peaks (Albrecht and Gotelli 2001). To our knowledge, little is known about ant seasonality in the tropics, but a recent study has found flooding during the wet season and high desiccation risk during the dry season as possibly responsible for reducing abundance in ants (Baccaro et al. 2012).

Ants attracted to baits vs. background diversity

Baits generally attract less species than other methods like pitfalls or winkler traps (Andersen 1991, Groc et al. 2007, Tista and Fiedler 2010). However, they present the advantage of being the fastest way to capture ants, and they can be used to obtain ecological and behavioural data. Baits have been used to assess dominance hierarchies, temporal differences of ant activity between periods and seasons (Delsinne et al. 2007, Arnan et al. 2012) and also trophic and microhabitat differences (Kaspari and Yanoviak 2000). In our study, the baits attracted 19 out of the 22 more common species with comparable or higher incidence (Bray-Curtis distance: 0.717), and 29 out of 47 species caught with pitfalls in total. For four of the eight baits, rarefaction and Chao species richness estimators suggested that additional species may still have been sampled (Table 1). Most of the species that were captured in pitfalls, but absent or rare at baits, were predators according to literature (genus *Pachycondyla* and *Anochetus*; Dejean et al. 1999) or fungus growers (*Atta, Cyphomyrmex*; Mikheyev et al. 2010), other species were with very few occurrences limiting their chances in occurring on the baits. We therefore suggest that their primary food sources were absent from the set of baits or inappropriately displayed. Many ant predators are solitary foragers, specialised on certain prey types, do not recruit, and immediately retrieve the whole food item to their nest instead of feeding directly at the spot (Dornhaus and Powell 2010). Thus, the chances of capturing such species without constant bait observation are smaller compared to species that recruit massively and do not retrieve large pieces of bait. *Pachycondyla crassinoda* for instance was only found twice on crickets and once on crushed insects but had a high pitfall incidence (Fig. 2). Therefore presenting suitable live prey species in an appropriate manner may prove difficult. For future studies, the set of baits should be continuously extended or amended with complementary baits and/or specific displays, aiming to cover as many species as possible.

Are specialisation, commonness and foraging efficiency interrelated?

The relationship between food specialisation and commonness has been explored in many taxa. Commonness can be defined in terms of geographic range, local abundance, or a combination of both (Kunin and Gaston 1993, Slatyer et al. 2013). Often, specialists are less abundant than generalists (Harcourt et al. 2002, Goulson et al. 2008), but specialisation can also be positively linked to local abundance (Blüthgen et al. 2007, Boulangeat et al. 2012). Here, we reasoned that species with a broader food niche should have a greater incidence than more specialized ones. In turn, more specialized species should be more efficient foraging for their required resources. The first prediction was rejected - commonness (measured as incidence) was not related to the degree of food or temporal specialisation. There were no common food specialists, as had been expected, but rare species included generalised and specialised ones (Fig. 4). Finally, we could show that specialised species tend to be more efficient foragers, as evidenced by the correlation between foraging efficiency (*fr)* and food specialization (*fs*).

Conclusions

The present study demonstrates that ant communities show temporal and trophic niche differentiation. Diurnal and nocturnal assemblages differed strongly, and assemblages at five different food items were significantly different from one another, although this difference was smaller than the temporal differentiation. On species level, in our range of baits, no correlation was found between species co-occurrence and niche specialisation. Significant preferences for food items and time periods were found for one-fourth to half of the species, and this would probably increase if sampling effort is intensified, including more different baits and additional time periods. However, while many species did have temporal and/or food preferences, no species showed strict temporal or dietary exclusiveness: the niches were broad enough to allow a certain variation in food resources and temporal activity. Such variation may be especially important for subordinate species, which can modify their dietary habits in presence of dominant species (Sanders and Gordon 2003). This niche 'plasticity' may be an important mechanism to reduce competition, and we interpret the temporal niche difference of species caught in pitfalls and at baits as evidence of such plasticity.

Future studies should aim at assessing niche differentiation in more detail. This could include different strata complimentary to ground sampling (subterranean; shrubs, tree trunks, canopy). It is likely that ants differ in further niche dimensions which are more difficult to assess, e.g. activity under different weather conditions. The community-based approach presented here may also be complemented by single-species assays in order to exclude the impact of competitors. We should bear in mind that niche differentiation is but one possible mechanism of species co-existence, and that the role of other factors, such as stochasticity in colony establishment success, dispersal and habitat disturbance must not be neglected (Andersen 2008, Arnan et al. 2011).

This chapter is based on an original research article under current revision in *Oikos.*

Chapter II. Compete or adapt: niche plasticity affects the functional traits of species in tropical ant assemblages.

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Key words
dietary specialisation; temporal specialisation; niche breadth; niche partitioning; co-occurrence analysis; coexistence mechanisms.

Abstract

Functional diversity is defined as “the value and range of the functional traits of the organisms in a given ecosystem”. The definition is sound but there has been confusion concerning the interpretation of the value and range of functional traits. Many studies implicitly assume that functional traits within a species are constant. However, intraspecific variance has been increasingly recognized as an important aspect of community ecology. Here, we studied dietary and temporal niches of ant species in a primary and a secondary tropical rainforest in Borneo. We tested whether dietary and temporal niches vary less within a species than across species, but predicted that competitively inferior (subordinate) species show higher niche plasticity than dominant ones, since they respond to the presence of competitors.

In each forest, we assessed the dietary and temporal niches of the species common to both sites. To this end, we offered seven different bait types (oleic was not considered in this manuscript) that reflected natural resources during day and at night. The competitive ability of each species was estimated using co-occurrence analyses.

Our results show that traits such as temporal and food preferences can shift drastically between two sites, to the extent where a species’ niche may be closer to that of another species than to its conspecific. Even dominant species showed different food or temporal preferences in the two sites. However, numerically dominant species displayed a lower overall niche plasticity than subordinates. We interpret this as a trade-off between the capacity to compete and the need to adapt.

Categorical functional traits should therefore be interpreted with caution. In contrast, multifactorial approaches based on continuous trait values permit a thorough quantification of a species’ niche plasticity that combines multiple functional traits. Knowledge about the niche plasticity of species within a community is important to predict their ability to cope with changing environmental conditions.

Introduction

An essential part of community ecology is to understand the processes that explain patterns of abundance and distribution of species (May and Arthur 1972). One of the main approaches to explain patterns of co-existence is the principle of limiting similarity. It states that competitive exclusion prevents the co-occurrence of species with too similar niches (Gause 1934; Morrison 1996), and that niche partitioning is a prerequisite for the coexistence of different species. However, many of the studies on this issue implicitly or explicitly assumed that species-specific traits are fixed and constant. Species coexistence should be enabled through differentiation in these traits (MacArthur and Levins 1967). Accordingly, many community ecologists have focused on average trait values per species, and considered differences in these values as the promoter of species diversity As such, average trait values are regularly used to assess functional diversity and to model ecosystem processes (Walker, Kinzig & Langridge 1999; Díaz & Cabido 2001; Bihn, Gebauer & Brandl 2010; Woodcock *et al.* 2013, Loreau 2010). However functional traits may vary more between than within species (McGill et al. 2006a, Cadotte et al. 2011). Organisms can adapt their individual niche according to the presence of competing species. Some species may show less niche plasticity than others – either because they do not need to change their niche, or because they cannot. Hence, functional trait values cannot be considered as fixed characteristics of a species, and it is necessary to consider the effect of trait evolution and plasticity in ecological studies (Berg and Ellers 2010).

Ants have diversified into tens of thousands of species, colonized most of the world’s terrestrial ecosystems, and acquired multifarious ecological roles (Ward 2013) and competition is considered as the “hallmark” of ant ecology (but see Cerdá, Arnan & Retana 2013). As such ants are an appropriate model system to investigate niche differentiation and competitive exclusion. As in many other taxa, they can be classified into dominant and subordinate species, where the dominant ones can exclude subordinates from their territory or resources (Cerdá et al. 2013). Some subordinate species avoid competition with dominant ants by reducing the temporal overlap (Human and Gordon 1996, Holway 1998), while others coexist temporally but limit their interactions (Human et al. 1998), as with resource partitioning. However, it is still largely unknown whether the degree of niche plasticity varies with competitive ability, i.e. whether competitively inferior species show higher plasticity than superior ones (but see Sanders &

Gordon 2003). Recent research even indicated that niches within species may vary as much as between species (Cadotte et al. 2011). Thus, community ecology needs to fully understand species niche plasticity and the potential consequences of the variation of traits in order to predict community response to change and the degree of stability of an ecosystem (Bolnick et al. 2011, Violle et al. 2012).

Here, we investigated how species shift their dietary and temporal niches between two different sites with high species overlap. We hypothesized that dominant species should be able to retain their traits, while subordinate species must adapt to the presence of dominants and change their traits accordingly. By applying the exact same sampling method on the two sites, we were able to measure temporal and dietary preferences among the ant species common to both sites. We analysed how consistent are qualitative ecological traits across sites. Furthermore, we tested whether traits varied more between than within species (McGill et al. 2006a), and expected the "ecological distance" (i.e. distance between niches) between conspecifics to be smaller than between species. Finally, we examined whether subordinate species alter their niche in order to coexist with highly competitive ones that can displace other species and thus retain their "optimal" niche.

Materials and Methods

Study sites and species studied

Niche plasticity was investigated in two paleotropical sites with differing ecological status. Sampling was performed in a primary forest of the Danum Valley Conservation Area (Sabah, Malaysian Borneo; 4°55′N-117°40′E). The site is part of a 438 km² primary forest dominated by Dipterocarpaceae trees. The second site was the Malua Forest Reserve (4º24′N-118°14′E) and is 22.6 km away from Danum Valley. It comprises 35 km² of production forest, which was selectively logged in the 1980s. We chose close by and similar forest habitats with different ecological status in order to have similar ant assemblages, but at the same time enhance the likelihood of having different niches for each species. Indeed, species composition was largely similar, with 50% of the species shared by both sites, but the ecological stability differed markedly (Houadria et al. 2015a). On each site, we established four plots (90 m²) of 4 x 4 grid points, i.e. a total number of 64 grid points. We presented seven baits at every grid point during day and at night, but only one bait at a given time. We used seven complementary food baits which reflected natural resources available to ants in a rainforest: sucrose, melezitose, crushed insects, bird faeces, a seed mixture, living termites and living grasshoppers (Houadria et al. 2015c).

Altogether, we captured 81 species, out of which 32 occurred in both sites. Since our analyses were based on species frequencies (i.e. the number of times a species was captured at any bait), we included only species with a frequency ≥ 7 in both sites. This criterion was fulfilled by eight species (Table 1).

Data analysis

Ecological traits across sites

For each species *n* with a frequency ≥ 7, food preferences and temporal niche were calculated separately for the two sites. Food preferences were calculated based on the total number of occurrences of every species on each of the seven baits. Then, the occurrences were randomly permuted 1000 times to assess on which bait the realized frequency was higher than expected from random (preferred bait). We calculated the quantile of the realized value against the null distributions, and deemed them significant if they fell outside the 95% confidence interval.

Temporal niche, tn_n , was calculated by comparing its total frequency during day and at night and was calculated as : $$tn_n = 2 \cdot \frac{fr_{day_n}}{fr_{day_n} + fr_{night_n}} - 1,$$

where tn_n is the temporal niche position, $fr_{day,n}$ and $fr_{night,n}$ are the total number of occurrences during day and night, respectively; *tn* ranges from -1 (purely nocturnal) to +1 (purely diurnal). Using χ^2 tests, we tested whether a species' temporal distribution significantly differed from random, i.e if it was significantly more present at day or night.

Niche plasticity

For each species and each site, we created a vector containing its relative frequencies on the 14 bait (7 night and day), such that the summed relative frequencies per site equaled 1. The niche plasticity of a species was then calculated as the Euclidean distance between its vectors for the two sites. Euclidean distance was considered more appropriate as it incorporates quantitative standardized values and joint absences whereas Bray-Curtis distance is more suitable for actual abundances.

Co-occurrence analyses

These analyses test for non-random patterns of species co-occurrence among the sampled ant communities (Gotelli 2000). We analysed co-occurrence separately for each bait type, time of day, and site, i.e. conducted 28 separate analyses. Each analysis was based on a presence/absence matrix where each grid point is a row (i.e. n=64) and each column is an ant species. For each ant species, we calculated the number of real associations as the number of times it co-occurred with any other species on the same bait. The occurrences of each species were then randomly assigned to the different grid points, such that the total number of occurrences per species is equal to those in the original matrix, but each grid point has the same probability of being assigned an ant occurrence (i.e. the fixed-equiprobable algorithm *sensu* Gotelli, 2000). We performed 1000 randomizations per analysis, and compared the real number of associations to the distribution of randomized values we had obtained. For each species, the segregation quantile was calculated as the proportion of randomized matrices where it had fewer co-occurrences with any other species than in the real dataset. We interpret these values as a measure of a species' ability to exclude other species. We calculated species-specific segregation values ($S_{\alpha kR}$) for each of the 28 matrices and considered segregation significant when the p-value was below 0.025. The overall species-specific segregation value S_i was calculated as the weighted mean of these 28 values, based on the idea that the higher the relative frequencies on a resource, the more relevant are these segregation values for this species.

$$S_i = \frac{\sum \left(S_{\alpha kR} \times N_{\alpha kR} \right)}{\sum N_{\alpha kR}}$$

Where S_i is the overall segregation values for species *i*, $S_{\alpha kR}$ the quantile value and $N_{\alpha kR}$ the frequency of species *i* for a given resource *R*, time α, and site *k*. The relation between a species' segregation value and its niche plasticity was tested using Spearman correlation. Temporal specialisation ranges from -1 (purely nocturnal), 0 (no specialisation) to 1 (purely diurnal). Wilcoxon signed-ranks test was used to evaluate if a species' temporal distribution significantly diverged from no specialisation, i.e if it was significantly more present at day or night.

Furthermore, we assessed whether a species significantly preferred a certain bait type. To this end, we randomly assigned a species' the summed frequencies to the seven different baits; we then calculated the quantile of the real value against these null distributions, and deemed them significant if they fell outside the 95% confidence interval. Numerically dominant species were defined as those with significantly higher incidence than the others (one tailed *t*-test). All computations were performed using R version 2.15.2 (R Development Core Team 2012).

Results

Table 1: Morphospecies included in this study, and their incidence (number of grid points where they were captured) in the two sites. Species in bold had higher incidence than other species in Danum and Malua, respectively (one-tailed *t* tests: *Carebara* sp.1: t = -3.812, p = 0.003 and t=-2,08, p=0,038; *Lophomyrmex* sp.1: t=-4,765,p=0,001 and t=-6,139, p < 0,001)

Subfamily	Morphospecies	Incidence	
		Danum	Malua
Formicinae	*Camponotus* sp.1	18	15
	Euprenolepis sp.1	15	11
Dolichoderinae	*Technomyrmex* sp.2	5	20
Myrmicinae	***Carebara* sp.1**	**50****	**35***
	***Lophomyrmex* sp.1**	**56****	**62*****
	Lophomyrmex sp.2	27	9
	Pheidole sp.6	20	6
	Recurvidris sp.2	17	11

Qualitative trait differentiation across sites

Food preferences

The most numerically dominant species, *Lophomyrmex* sp.1, showed the same dietary characteristics for both sites with preferences for crushed insects, melezitose and sucrose (Fig. 1). Most of the other species only showed significant food preferences in Danum. The second most dominant species, *Carebara* sp.1, preferred seeds; *Eupronolepis* sp.1 preferred sucrose and *Pheidole* sp.6 melezitose. Only *Technomyrmex* sp.1 had a preference for both carbohydrates in Malua but not in Danum. Neither *Camponotus* sp.1 nor *Pheidole* sp.6 showed any food or temporal preferences regardless of the site.

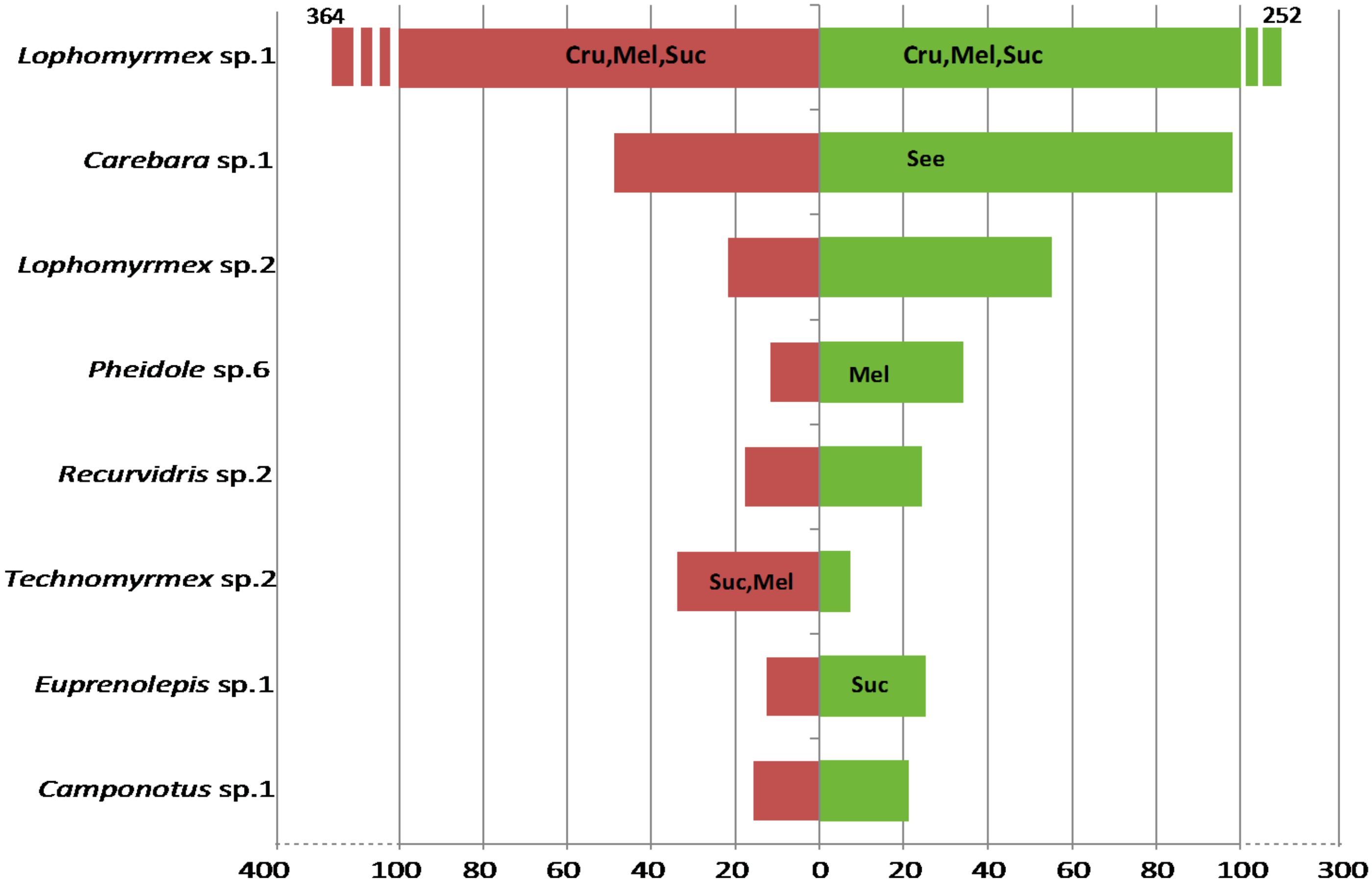

Fig. 1 Total frequencies per species on all bait types for Danum (green) and Malua (red). For species with significant food preferences, the preferred baits are given: *Cru* (crushed insects), **Suc** (sucrose), **See (**seeds) and **Mel** (melezitose).

Temporal preferences

Although none of the species showed opposite temporal specialisation in the two sites, the temporal niche often differed between Danum and Malua (Fig. 2). *Carebara* sp.1 and *Technomyrmex* sp.2 were marginally nocturnal in Danum, but unspecialised in Malua, and the reverse scenario was found for *Eupronolepis* sp.1. *Lophomyrmex* sp.1 was significantly diurnal in Danum, but temporally unspecialised in Malua. Only *Recurvidris* sp.2 showed the same diurnal specialisation in both sites (albeit marginal in Malua).

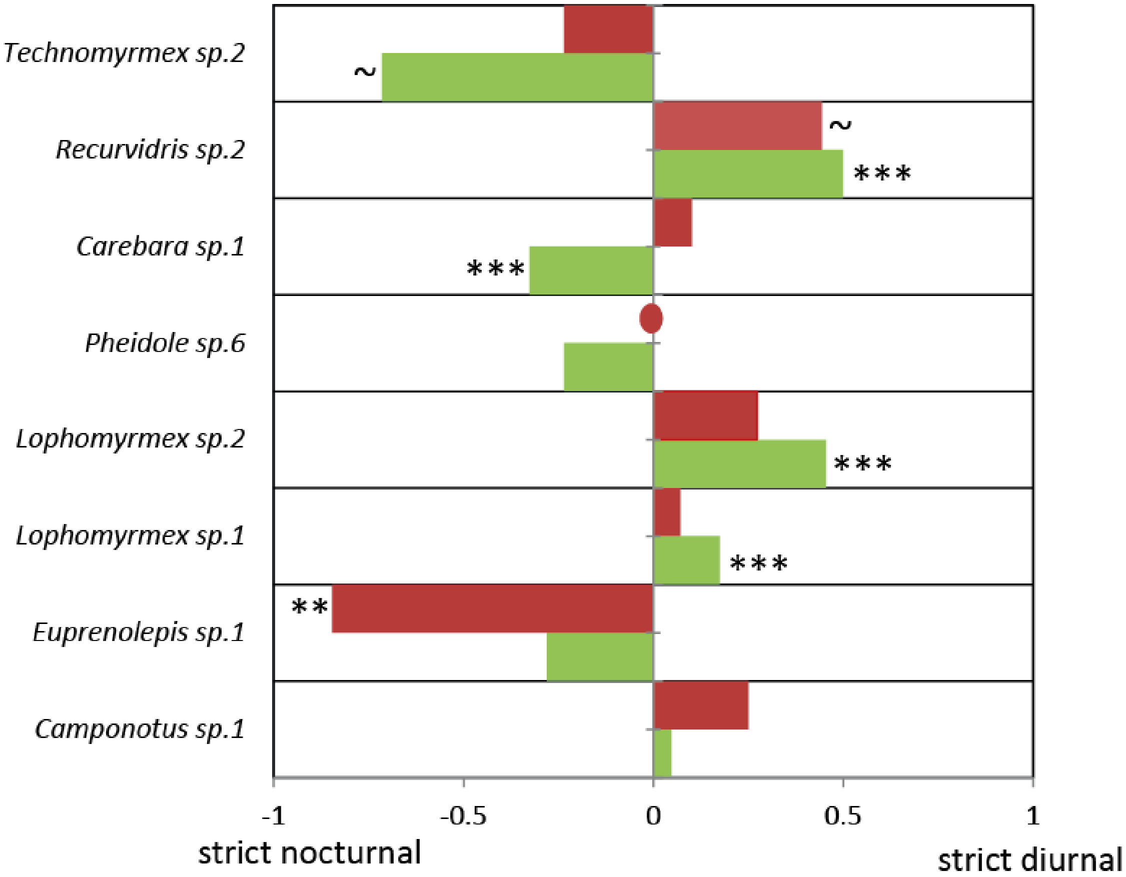

Fig. 2 Temporal niche (*tn*), separately calculated for Danum (green) and Malua (red). Significant temporal specialization (according to χ^2 test) is indicated with asterisks: *p < 0.05; **p < 0.01; ***p < 0.001. Full circles indicate a temporal niche of zero.

Niche plasticity

Fig. 3 illustrates the Euclidean distance of conspecific and interspecific niches between different sites. The two numerically dominant species, *Lophomyrmex* sp.1 and *Carebara* sp.1, showed the lowest niche plasticity (Fig.3), followed by *Lophomyrmex* sp.2. In these two species, conspecific niche distance between Danum and Malua was smaller than the distance to any other species (Table S1). In contrast, the species with highest niche differences between sites were *Euprenolepis* sp.1, followed by *Pheidole* sp.6 and *Technomyrmex* sp.2.

Camponotus sp.1, *Recurvidris* sp.2, *Lophomyrmex* sp.1, sp.2, *Carebara* sp.1 and *Technomyrmex* sp.2 (but marginal) were closer to their conspecific than other species and *Eupronolepis* sp.1 and *Pheidole* sp.6 were not (Table S1). We notice that *Technomyrmex* sp.2 in Malua is more similar to 5 species in Danum than to its conspecific. *Euprenolepis* sp.1 and *Pheidole* sp.6 in Danum are respectively more similar to six and five species in Malua than to their conspecific. Only the two most numerically dominant species, *Lophomyrmex* sp.1 and *Carebara* sp.1 are never more similar to other species niches.

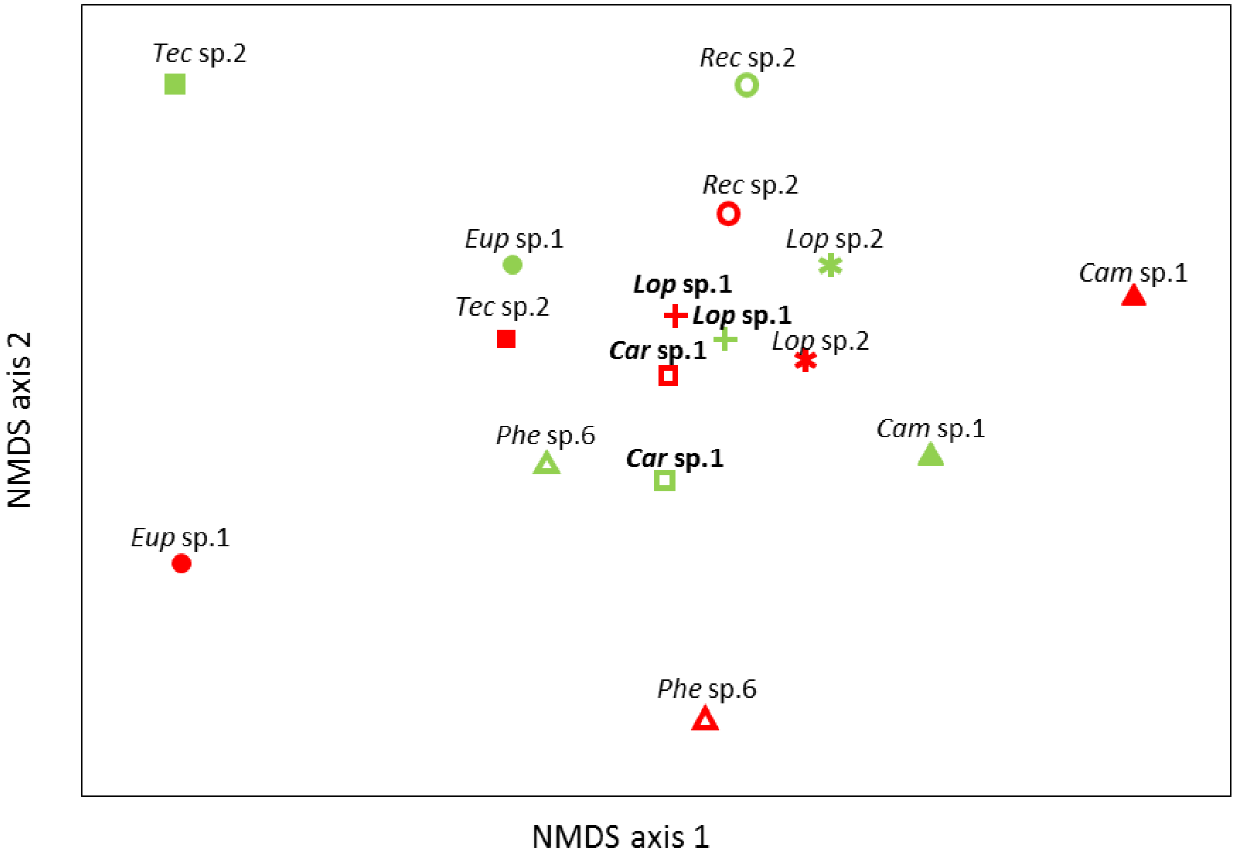

Fig. 3 NMDS ordination (stress: 0.11) of niche positions in the two sites. The ordination is based on the frequency of each species at the seven baits during the two time periods. Each shape represents one species; green and red refer to the niche in Danum and Malua, respectively. The two most common species are shown in bold. *Lop*: Lophomyrmex; *Cam*: *Camponotus*; *Car*: *Carebara*; *Rec*: *Recurvidris*; *Eup*: *Euprenolepis*; *Tec*: *Technomyrmex*; *Phe*: *Pheidole*.

Segregation species level

Table 2: Number of times when a species showed significant segregation according to co-occurrence analysis at a given bait and time of day. NRA: number of realized associations, *p* values represent the percentage of randomized associations smaller or equal to those of the real matrix (significant if < 0.025). Cru: crushed insects, Mel: melezitose, Suc: sucrose, See: seeds, Ter: termite. *Lopho: Lophomyrmex, Careb: Carebara.*

Site	Time	Bait	Species	Occurrences	NRA	*p*
Danum	Day	Cru	*Lopho* sp.1	33	8	<0.001
	Day	Cru	*Lopho* sp.2	11	2	<0.001
	Day	Mel	*Lopho* sp.1	31	9	<0.001
	Day	Mel	*Lopho* sp.2	5	1	0.014
	Day	See	*Lopho* sp.2	4	0	0.025
	Day	Suc	*Lopho* sp.1	32	16	<0.001
	Day	Suc	*Careb* sp.1	8	4	0.012
	Day	Suc	*Lopho* sp.2	7	3	0.021
	Day	Ter	*Lopho* sp.1	22	6	0.020
	Day	Ter	*Lopho* sp.2	7	2	0.021
	Night	Cru	*Lopho* sp.1	22	4	<0.001
	Night	Cru	*Careb* sp.1	13	2	0.001
	Night	Mel	*Lopho* sp.1	19	10	0.001
Malua	Day	Cru	*Lopho* sp.1	44	5	<0.001
	Day	Cru	*Lopho* sp.1	44	5	<0.001
	Day	Mel	*Lopho* sp.2	2	0	0.015
	Day	Mel	*Lopho* sp.1	45	15	0.020
	Day	Suc	*Lopho* sp.1	39	11	<0.001
	Night	Cru	*Lopho* sp.1	40	11	<0.001

S_i was positively correlated to niche plasticity (Spearman correlation: ρ = 0.81, S = 16, p = 0.022), indicating that species with low niche plasticity have a high segregation capacity (Fig. 4).

Danum and Malua had respectively 13 and 6 cases where $S_{\alpha kR}$ was significant, i.e a species co-occurred with other species less often than expected (Table 2). Overall more cases were found for day time (chi^2 test: chi^2 = 6.37, df = 1, p = 0.012) and the majority of the resources concerned were crushed insects (37%), melezitose (26%) and sucrose (21%). Among the selected species, only three showed segregation, of which 11 cases were represented by *Lophomyrmex* sp.1, 6 cases by *Lophomyrmex* sp.2, and two cases by *Carebara* sp.1 (only in Danum).

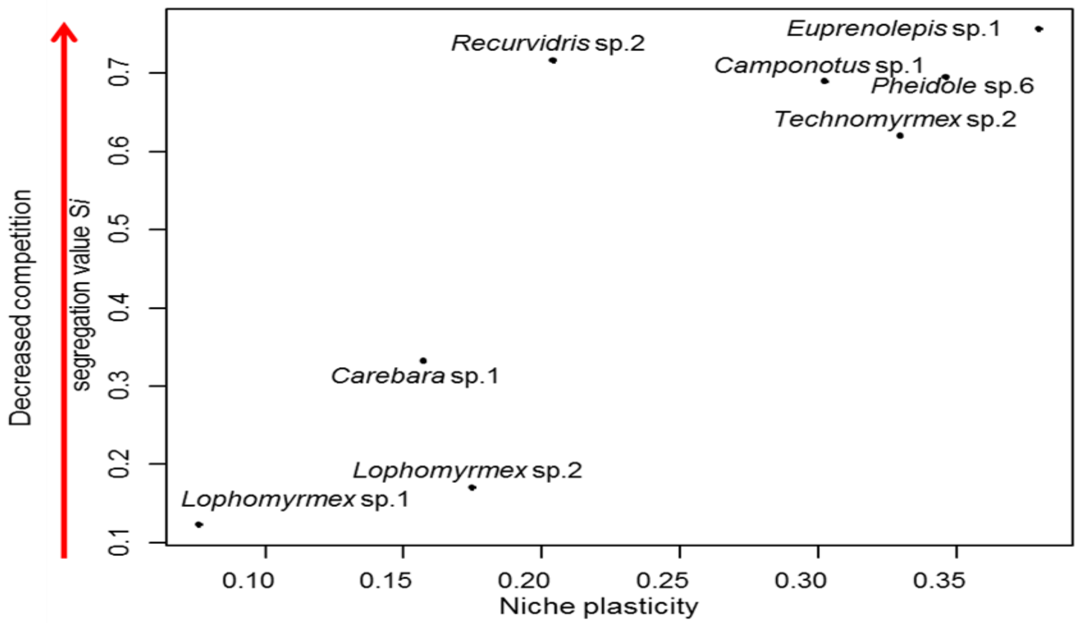

Fig. 4 Species-specific segregation value (S_i) plotted against niche plasticity (Euclidean distance between the niche in Danum and Malua). The correlation is significant (S = 16, p-value = 0.02 Spearman's rho = 0.81).

Discussion

Functional diversity is defined as "the value and range of the functional traits of the organisms in a given ecosystem" (Loreau et al. 2001). The definition is sound, but there has been much confusion concerning the interpretation of the value and range of functional traits. One of the main reasons is the lack of information on functional parameters (Hodapp et al. 2013) which ecological indexes are based on, and where generalizations on ecosystem functioning are still employed (Mouillot et al. 2005). As a consequence of these approaches, a general ecological understanding of trait variation across ecologically relevant spatial and temporal scales is lacking (Messier et al. 2010).

This study establishes that traits such as temporal and food preferences can shift considerably between sites, to the extent where a species' niche may be closer to another species than to its conspecific on another site. Additionally, we demonstrate that numerically dominant species displayed the lowest niche plasticity but do not necessarily show the same level of competitive exclusion depending on the site. Finally, our results demonstrate that species with high segregation capacity showed low niche plasticity.

Trait values across sites

Most species which showed food preferences were not consistent for both sites. This questions the categorization of food preferences as a trait (McGill et al. 2006a). Among the numerically dominant *Carebara* sp.1 did show a preference for seeds in Danum, but only *Lophomyrmex* sp.1 showed similar dietary preferences in both sites. This is consistent with previous research, where mostly subordinate species tend to shift their dietary preferences in the presence of dominant species (Wisheu 1998, Sanders and Gordon 2003). Nevertheless, the two dominant species did show temporal shifts, while two subordinate species (*Pheidole* sp.6 and *Camponotus* sp.1) did not display significant shifts in their food or temporal preferences, despite which their overall niche plasticity (combining time and diet) was higher than certain species which did. This highlights the importance of multifactorial approaches based on continuous values which permits quantification of the relative effect of several factors in a single ecological value (Agrawal and Ackerly 2007). Moreover *Carebara* sp.1, only showed segregation capacity, in one site. Hence, grouping species according to their competitive ability (Savolainen and Vepsäläinen 1989, Hölldobler and Wilson 1990, Andersen 1995) may be misleading as it can differ depending on the ecological context (Wiescher et al. 2011). The fact that the more competitive species showed less niche plasticity (Sanders and Gordon 2003) evokes a hierarchical relation between the capacity to compete and the need to adapt.

Dominant versus subordinate

The stronger segregation by dominants for day time in Malua could explain that the only temporal preferences found for any subordinate species was for night time (*Euprenolepis* sp.1). This corresponds to the one-side preferences concept where some species modify their preferences in order to coexist with dominant species which do not (Wisheu 1998). In the same line of thought we would expect there to be no species with similar food preferences as the dominant species. Only the dominant *Lophomyrmex* sp.1 showed a significant preference for crushed insects, whereas carbohydrates were preferred by dominant as well as subordinate species. This is concordant with the fact that nitrogen sources are often scarcer than carbohydrates (Davidson 1998), hence a resource worth more competing for. This may also explain why most segregation was found on crushed insects. The most dominant species, *Lophomyrmex* sp.1, was the only one to show the same food preferences in both sites, which concurs with our prediction that competitive dominance and observed niche plasticity, are negatively related.

Dominant versus dominant

Among the competitors in Danum, we found evidence for "competing and adapting": species segregation was stronger than in Malua, and species showed stronger niche partitioning. In Danum, the two most dominant species showed opposite temporal specialisation, different food preferences, and strong segregation (Fig. 1-2; Table 2). This evokes centrifugal organization of a community (Wasserberg and Kotler 2006), where increased competition creates a standoff, niche preferences are split and each species occupies the portion where it is the superior competitor. However, in Malua the same species were temporally generalized and showed fewer cases of segregation. Similarly, *Lophomyrmex* sp.2 was significantly diurnal in Danum but temporally generalised in Malua, and showed segregation on more resources in Danum than in Malua.

The use of functional traits in conservation

To be useful to community ecology traits should vary more between than within species and preferably be measured on continuous scales. The fact that certain species show more similarity to other species than conspecifics highlights the importance of niche plasticity in defining functional traits, whereby the niche plasticity of a species can alter its ecological function in a given community. Numerically dominant species are often central in the stability of an ecosystem (Cardinale et al. 2006). In our study, they were the species with low niche plasticity, but nevertheless varied in temporal preference, segregation capacity, and, to a lower degree, food preference. This, in spite of the fact that Malua and Danum were only 22.6 km away from each other and were originally connected through a contiguous habitat.

Conclusion

This experimental study supports the theory that numerically dominant species tend to compete whereas subordinate species tend to adapt by shifting their ecological niche (Sanders and Gordon 2003). However, among highly competitive species, the strategy shifts to niche partitioning and points towards a centrifugal organization.

Based on the three ecological aspects, i.e. resource preferences, temporal breadth and segregation capacity, we have shown that trait plasticity can affect the functional trait of species. This, in turn may have a preponderant role in ecosystem stability as for instance, functional redundancy an aspect which will be further discussed in the next chapter. However, our study only considered a limited number of traits. Research in the past has demonstrated that traits such as thermal tolerance (Bestelmeyer 2000), desiccation resistance (Arnan et al. 2012) may also play and important role in species coexistence. Community ecology needs to fully understand – and quantify – niche plasticity and the potential consequences of intraspecific trait variation (Bolnick et al. 2011, Violle et al. 2012). More empirical studies are required that focus on the factors that determine shifts in the realised niches, as to fully understand the influence of interspecific interactions on niche plasticity. In order to incorporate trait plasticity to theoretical models which predict ecosystem stability and community responses to environmental change.

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Chapter III: The relation between circadian asynchrony, functional redundancy and trophic performance in tropical ant communities

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Abstract

The diversity-stability relationship has been under intense scrutiny for the past decades, and temporal asynchrony is recognized as an important aspect of ecosystem stability. In contrast to relatively well-studied inter-annual and seasonal asynchrony, few studies investigate the role of circadian cycles for ecosystem stability. Here, we studied multifunctional redundancy of diurnal and nocturnal ant communities in four tropical rainforest sites. We analyzed how it was influenced by species richness, functional performance, and circadian asynchrony. In two neotropical sites, species richness and functional redundancy were lower at night. In contrast, these parameters did not differ in the two paleotropical sites we studied. Circadian asynchrony between species was pronounced in the neotropical sites, and increased circadian functional redundancy. In general, species richness positively affected functional redundancy, but the effect size depended on the temporal and spatial breadth of the species with highest functional performance. Our analysis shows that high levels of trophic performance were only reached through the presence of such high-performing species, but not by even contributions of multiple, less efficient species. Thus, these species can increase current functional performance, but reduce overall functional redundancy. Our study highlights that diurnal and nocturnal ecosystem properties of the very same habitat can markedly differ in terms of species richness and functional redundancy. Consequently, like the need to study multiple ecosystem functions, multiple periods of the circadian cycle need to be assessed in order to fully understand the diversity-stability-relationship in an ecosystem.

Introduction

The stability of ecosystems has been defined as low fluctuations over time (temporal stability), recovery speed after disturbance (resilience), a system's ability to maintain its original state after disturbance (resistance) and finally, as its ability to buffer the loss of species (functional redundancy, which is the focus of this study) (Loreau 2010). It has become an area of intense research since anthropogenic loss of diversity started to threaten ecosystem services important to humans (Schwartz et al. 2000, Balmford et al. 2003). Whether biodiversity loss will inevitably result in loss of stability has been addressed by a wide range of studies across different ecosystems (Walker et al. 1999, Loreau et al. 2001, Steudel et al. 2012). Generally, species richness has a positive effect on ecosystem stability (Naeem 1995), and this effect is especially strong if multiple ecosystem functions are considered simultaneously (Hector and Bagchi 2007, Gamfeldt et al. 2008, Isbell et al. 2011).

Biodiversity can stabilize ecosystem functioning by making it less vulnerable to varying population sizes of individual species (Thibaut and Connolly 2013). If the populations of different species fluctuate asynchronously through time, the sum of their populations, and thereby their total functional contributions, varies less over time than that of any single species (Doak et al. 1998, Yachi and Loreau 1999, Loreau 2010, Garibaldi et al. 2011). Such temporal asynchrony can be manifested on multiple scales, e.g. as inter-annual variation, seasonal, and circadian cycles. As most work was conducted on plants, for which seasonal and inter-annual changes are most important (Isbell et al. 2011), few studies have investigated the role of circadian cycles for ecosystem functioning (but see Andresen 2002, Boulay et al. 2007). However, in taxa which include diurnal, nocturnal and diel species, their activity distribution over the circadian cycle influences the overall contribution of the taxon to ecosystem functioning. If functions are taken over by different species during different time periods, the stability of the whole system increases since the functions rest on more species.

A key aspect of the diversity-stability relationship is the concept of functional redundancy (FR). It is defined as the number of species contributing to an ecosystem function (Lawton et al. 1993), and implies that the presence of multiple, functionally similar species can compensate for the decline or extinction of functionally relevant species after environmental change (Rosenfeld 2002a, 2002b). Hence, high functional redundancy increases the overall stability of ecosystem function since the functions rest on more species (Walker et al. 1999). How similar do species have to be for being considered functionally similar? Functional redundancy can vary depending on the number of functions or functional traits distinguished by the researcher (Petchey and Gaston 2002, Rosenfeld 2002a). Many studies therefore measured functional diversity rather than functional redundancy. Such metrics are based on functional groups, morphological characters, phenology, life-history traits and food web complexity (Walker et al. 1999, Díaz and Cabido 2001, Bihn et al. 2010, Woodcock et al. 2013). Although the advantage of such methods lies in the straightforward approach of focusing on the functional divergence between species (Mason et al. 2005), it remains unclear which of the traits are actually relevant for ecosystem functioning (Hodapp et al. 2013). Here, we therefore introduce a reversed approach where, instead of analyzing how many specific functional traits a given species presents, we study seven *a priori* defined ecosystem functions and assess each species' contribution to them in order to calculate functional redundancy.

The goal of this study was to investigate which factors influence multifunctional redundancy in tropical ant communities, with a focus on circadian cycles. Ants represent one of the most diverse and abundant animal taxa in tropical rainforests and are 'ecosystem engineers'. Due to their high overall biomass, probably one of their most important impacts on ecosystem processes happens through their consumption of resources, e.g. predation, nectarivory, granivory and scavenging. The latter is related to detritivory, for which ants also play an important role in the nutrient cycle (Folgarait 1998b). Here, resource consumption can be regarded as a measure of functional performance, analogous to primary production in plants. Contrary to the agricultural concept of overyielding where factors that increase performance are the main research goal (Hector 2006), our focus is on the relation between functional performance and stability. High functional performance in an ecosystem can be sustained either by relatively even contributions of many species, or by outstanding functional performance of a single species, which dwarfs the contribution of the others (Grime 1998). Thus, the evenness of functional contributions, and its relation to overall functional performance can affect functional redundancy (Fig. S1).

Since assessing single ecosystem functions can be misleading (Hector and Bagchi 2007, Gamfeldt et al. 2008, Byrnes et al. 2014), we measured average redundancy for seven different functions, all of which are related to resource consumption. In order to assess the generality of our results, we studied forests that differed in biogeographic region and disturbance status. To obtain an accurate estimate of each species' performance on multiple functions, we incorporated empirically measured functional traits such as biomass, recruitment and spatial frequency in our calculation of functional redundancy. We analyzed the impact of species richness and functional (trophic) performance on functional redundancy, and tested whether these impacts differ between sites and between diurnal and nocturnal ant communities. A special focus was placed on the contribution of the highest-performing species. We then studied the effects of daytime, species richness and trophic performance on FR. If, at high levels of species richness, high trophic performance is mainly due to single, high-performing species, we should expect a decreasing functional redundancy ('sampling effect', Cardinale *et al.* 2006). In a subsequent step, we analyzed the increase in functional redundancy by shifting from one time period to the whole circadian cycle. We tested whether the increase was determined by species richness, circadian asynchrony, and/or functional performance at grid point level.

Materials and Methods

Study sites and sampling design

Ant ecosystem functions were investigated in two neotropical (French Guiana) and two paleotropical sites (Borneo). On each continent, we sampled a primary and a secondary forest, henceforth abbreviated as NPF (neotropical primary forest), PSF (paleotropical secondary forest) and so on. In the neotropics, the Les Nouragues Nature reserve was studied as primary forest (NPF, 4°05′N-52°41″W), which covers more than 100.000 ha of pristine forest. The secondary forest site was a 16 ha forest fragment, bordered by urban grass and surrounded by residential areas on the Campus Agronomique in Kourou (NSF, 5°09′N-52°39″W). In the paleotropics, primary forest was sampled in the Danum Valley Conservation Area (PPF, Sabah, Malaysian Borneo; 4°55′N-117°40′E). The site is part of a 438 km² primary forest dominated by Dipterocarpaceae trees. As secondary forest, the Malua Forest Reserve was chosen (PSF, 4º24′N-118°14′E). It comprises 35 km² of production forest, which was selectively logged in the 1980s.

On each site, we established four plots (90 m²) of 4 x 4 grid points, i.e. a total number of 64 grid points. Sampling was performed using pitfalls and seven different baits. We presented seven baits and three pitfalls at every grid point during day and at night, but only one bait or one pitfall at a given day (Andersen 1994). We used seven complementary food baits which reflected natural resources available to ants in a rainforest: sucrose, melezitose, crushed insects, bird faeces, a seed mixture, living termites and living grasshoppers (Houadria et al. 2015). See supplement for more details on the sites and the sampling methods. In the context of our study, we define ecosystem functions as the consumption rate of these resources; each resource type is assumed to represent one function.

Data analysis

Defining the trophic performance of a species for a specific resource

To estimate the relative contribution of a species *i* to the consumption of a resource α, we calculated its species- and resource-specific trophic performance as

$$\text{eqn.1: } sTP_{i,\alpha} = M_i^{3/4} \cdot W_{i,\alpha} \cdot AR_{i,\alpha} ,$$

where M_i is the dry mass of species *i*, $W_{i,\alpha}$ is the median number of workers of species *i* at resource α, and $AR_{i,\alpha}$ is the attraction rate of species *i* to resource α. According to metabolic theory, the resource quantity consumed by any animal, i.e. its consumption rate, is proportional to the 3/4th power of its biomass *M* (Allen et al. 2002). $W_{i,\alpha}$ is an estimate of how much species *i* recruits to resource α, and was calculated to reduce variation from stochastic factors like nest proximity or the time elapsed since a resource was discovered. The attraction rate was an estimate of the likelihood that species *i* would recruit to resource α given its presence on a grid point, and was calculated as

$$\text{eqn.2, } AR_{i,\alpha} = \frac{f_{i,\alpha}}{J_i}$$

where $f_{i,\alpha}$ denotes the number of times it was found foraging on a resource α during day or night (range 1-128) and J_i is its incidence, i.e. the number of grid points where it was found at least once in pitfalls or baits (range 1-64). For J_i, since both methods were complimentary in sampling additional species on certain gridpoints, data from baits and pitfalls were combined to obtain the most precise information on a species' spatial presence. Incidences at pitfalls and incidences at pitfalls and baits combined were highly correlated for all four sites (Fig. S4). Hence, combining the two methods did not favour certain species, or bias the metric towards bait data. The attraction rate is low for a common species that rarely recruited on a resource, but high for a rare species that always recruited.

Calculating functional redundancy

Functional redundancy for a single resource α at grid point k and time t ($\text{SFR}_{\alpha,k,t}$) was calculated as its effective number of species, where each species was weighted according to its trophic performance $sTP_{i,\alpha}$. We included $sTP_{i,\alpha}$ of all species caught at grid point k during time t in any bait or pitfall. This way, we used information about the presence of less efficient and potentially behaviourally non-dominant species, such that competitive exclusion from a single bait should not affect our estimate of functional redundancy. We first calculated the single-function Shannon entropy (i.e. Shannon diversity) of these trophic performances for resource α at grid point k and time t as

$$SH_{\alpha,k,t} = -\sum_{i=1}^{I_{k,t}} \frac{sTP_{i,\alpha}}{gTP_{\alpha,k,t}} \cdot \ln\left(\frac{sTP_{i,\alpha}}{gTP}\right)_{\alpha,k,t} \qquad \text{eqn.3}$$

where $sTP_{i,\alpha}$ is the species- and resource-specific trophic performance of species *i* for resource α; $I_{k,t}$ is the number of species occurring at grid point *k* during daytime *t*; and $gTP_{\alpha,k,t}$ is the grid point-and resource-specific sum of trophic performances for all species at grid point *k* for resource α and time *t:*

$$gTP_{\alpha,k,t} = \sum_{i=1}^{I_{k,t}} sTP_{i,\alpha} \qquad \text{eqn. 4}$$

Shannon entropy reflects the uncertainty in the outcome of a sampling process (Walker et al. 1999) and is a commonly used diversity measure in ecology. Eqn. 3 calculates Shannon diversity of the relative functional contributions of all species at a grid point. Single-function redundancy was calculated as its exponential form: $sFR_{\alpha,k,t} = e^{SH_{\alpha,k,t}}$. eqn.5

This term expresses the 'effective' number of species fulfilling the function. Such an effective number reflects the relevance of different trophic performances in a community more accurately than the Shannon entropy (eqn. 3) itself would (Jost 2006). If trophic performance was equal for all species, $sFR_{\alpha,k,t}$ would equal the species richness for function α, but it is lower if species contribute unevenly. Multifunctional redundancy ($FR_{k,t}$, henceforth, ‘functional redundancy’ or ‘FR’) on grid point *k* and time of day *t* was calculated as the mean of the single-functional redundancies ($sFR_{\alpha,k,t}$) of the seven resources.

Statistical analysis

First, we compared species richness, functional redundancy between sites using ANOVA and Tukey HSD tests. Comparisons between diurnal, nocturnal and circadian (for day and night communities pooled) values were conducted using paired *t* tests. For each site, we determined the single highest-performing species based on its overall (site-level) trophic performance across all grid points. Such a species had high species-specific trophic performance coupled to high spatial frequency. We tested whether trophic performance and functional redundancy were higher on grid points with or without this species using Wilcoxon tests. Furthermore, temporal specialization of this species was assessed by comparing the number of grid points where it was captured during day and at night with χ^2 tests.

Subsequently, we analyzed which factors affect $FR_{k,t}$. We used a linear mixed-effects model, with $FR_{k,t}$ as response variable, grid point k as random factor, and the following fixed effects: local species richness $I_{k,t}$ (i.e. total number of species which were found at baits and pitfalls), multifunctional trophic performance $TP_{k,t}$, time of day t, and site (PSF, PPF, NSF, or NPF). $TP_{k,t}$ was calculated as the total trophic performance per grid point and daytime that was done by all species for all seven functions; values were standardized to account for variation in overall functional performance between sites, resources, and times of day. All metrics were calculated for each site separately. Due to interactions of ‘site’ with other factors in a comprehensive model (Table S3), we analysed each site separately.

In a further analysis, we asked which factors affect the grid point-wise gain in functional redundancy (ΔFR_k) accomplished through combining nocturnal and diurnal ant communities. The response variable was ΔFR_k, i.e. the increase in FR from the circadian cycle (pooled diurnal and nocturnal communities) compared to the average of diurnal and nocturnal FR. This gain might be affected by local species richness, the overall trophic performance $TP_{k,t}$ of all species present at a grid point, and the functional circadian asynchrony CA_k between species. CA_k was calculated as the Bray-Curtis distance between the species present during day or night at the same gridpoint. To account for interspecific differences in functional performance, we used species-specific trophic performance values instead of presence/absence values. If trophic performance was equal for all species, asynchrony would equal the β diversity between day and night based on presence/absence data. Like for functional redundancy and species richness, ΔFR and circadian asynchrony were first compared between sites using ANOVA and Tukey HSD. We then constructed a linear model with ΔFR as response variable and circadian asynchrony CA_k, trophic performance TP_k (summed over the two time periods), and species richness I_k as explanatory variables. Due to interactions of 'site' and other variables in a comprehensive model (Table S5), we calculated site-specific models.

In each model, interactions between all explanatory variables were allowed. Higher-level interactions were removed from the models if not significant. The importance of each factor or interaction was evaluated using χ^2 tests (FR, linear mixed-effects models) or F tests (ΔFR, linear models). For PSF, two grid points with outstanding trophic performance (up to five times the average $TP_{\alpha,k,t}$) were removed from the models. These points were the only ones to significantly affect any model when omitted. All analyses were conducted using R version 2.15.2 (R Development Core Team 2012). Regression planes were created using the *effects* package for R (Fox 2003).

Results

Species richness and high performing species across sites

The four rainforest sites differed in local species richness and the presence of high performing species (Fig. 1a, Table S1, S2). Among the four sites, the paleotropical secondary forest (PSF) showed the lowest species richness per grid point regardless of time period, although it had the highest species richness at the site level (Fig. 1a). The paleotropical sites were dominated by a single *Lophomyrmex* species. The species occurred in PPF and PSF on 60 and 62 gridpoints (respectively) out of 64, and accounted for 57% of the overall trophic performance in both sites (Fig. 2, blue species, Fig. S4). The highest performer in NPF was *Camponotus femoratus* (40% of total performance), it occurred only on 32/64 grid points. In NSF, it was another *Camponotus* species which occurred on 52/64 grid points. This species accounted for 46% of the total performance, but was mainly present at night (Fig. 2, green species). Grid points where the high performing species was present had a higher trophic performance in PSF (W = 65, $P = 0.014$), NSF (W = 750, $P = 0.0024$) and NPF (W = 723, $P < 0.0001$), but not in PPF (W = 694, $P = 0.15$). However, the dominance of such key performers was not necessarily associated with a loss in functional redundancy (all $P > 0.2$, except NPF with W = 1604, $P = 0.035$). The high-performing species was temporally specialized only in NSF (nocturnal; $\chi^2 = 17.8$; $P < 0.0001$; other sites: all $\chi^2 < 1.7$; $P > 0.19$)

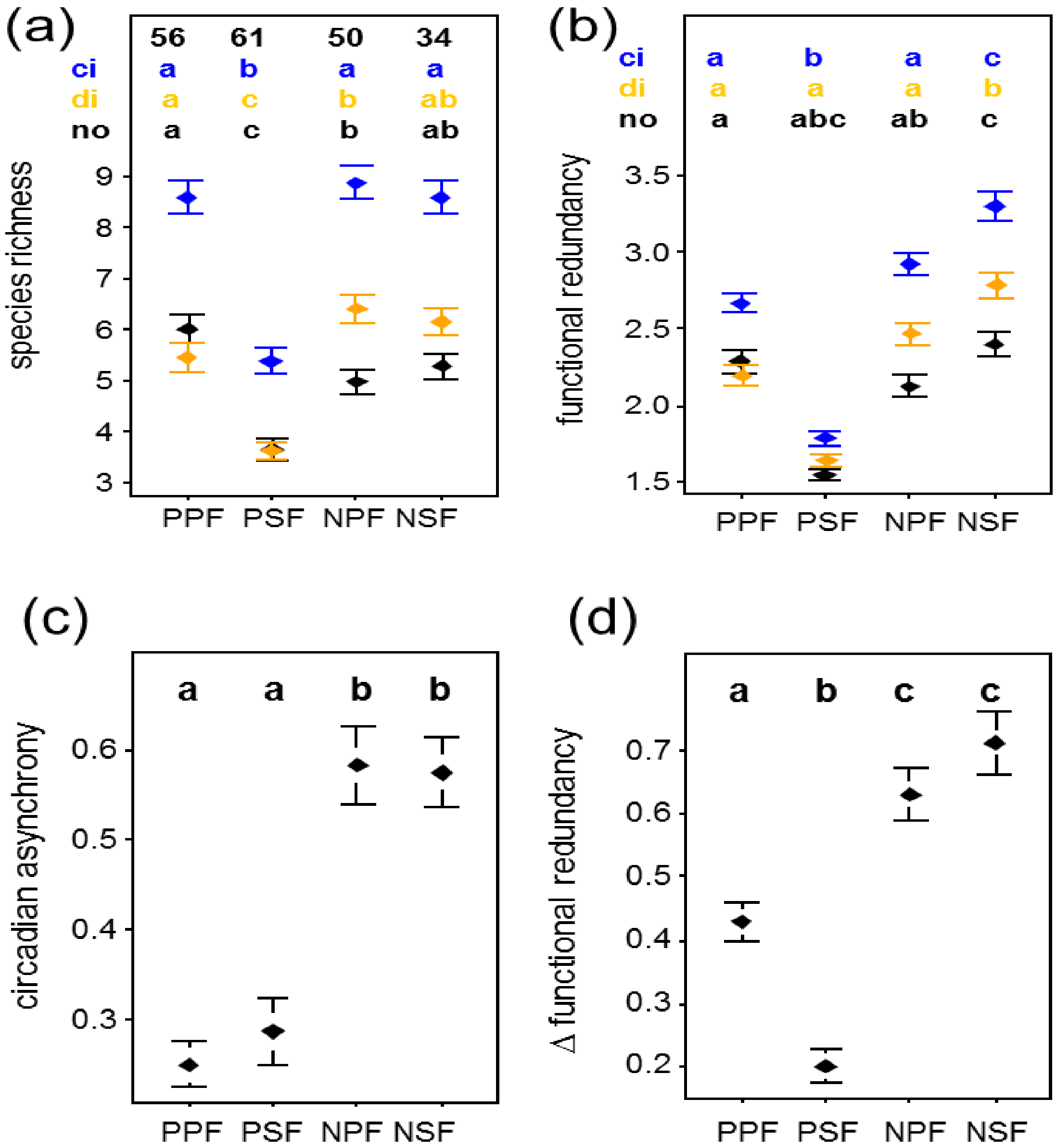
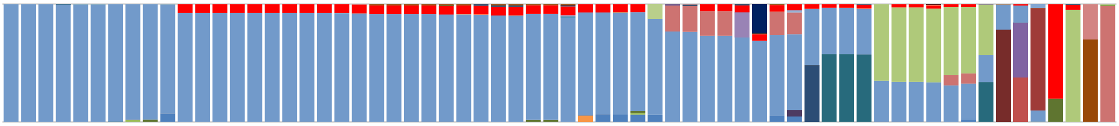
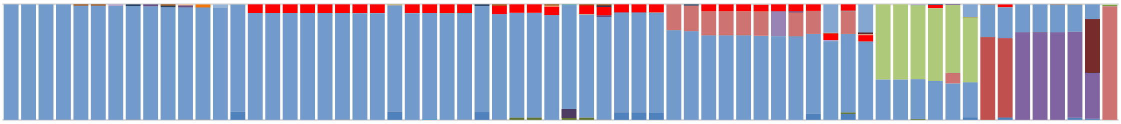


Fig. 1 (a) Species richness, (b) functional redundancy, (c) circadian asynchrony, and (d) circadian gain in functional redundancy per grid point in PPF, PSF, NPF and NSF. The graphs show mean and standard error. Sites with same letters are not significantly different according to Tukey HSD.The numbers above the plots in (a) give the site-level species richness. (a)-(c): Each graph shows circadian (CI, blue), diurnal (DI, orange) and nocturnal (NO, black) values. Nocturnal and diurnal species richness, and nocturnal and diurnal FR differed for NPF and NSF (paired *t* test: $p < 0.001$), but not for PPF and PSF ($p > 0.05$). For species richness and FR, both nocturnal and diurnal values differed from circadian ones for all four sites (paired *t* tests: all $p < 0.0001$).

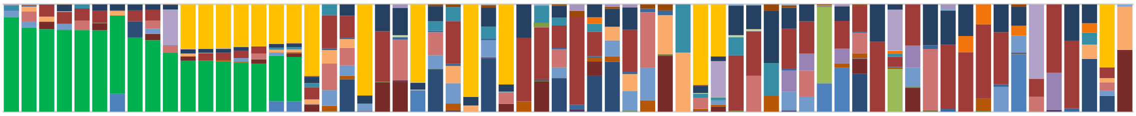
(a) PSF (day)



(b) PSF (night)



(c) NSF (day)



(d) NSF (night)

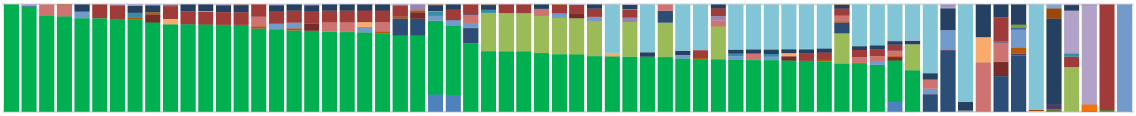


Fig. 2. Relative contributions of different species to trophic performance per grid point in PSF and NSF for different time frames. Each bar represents one of the 64 grid points; every color per site represents a different species. The bars are ordered left to right by maximum to minimum contribution of the highest-performing species.

Functional redundancy and circadian dynamics across sites

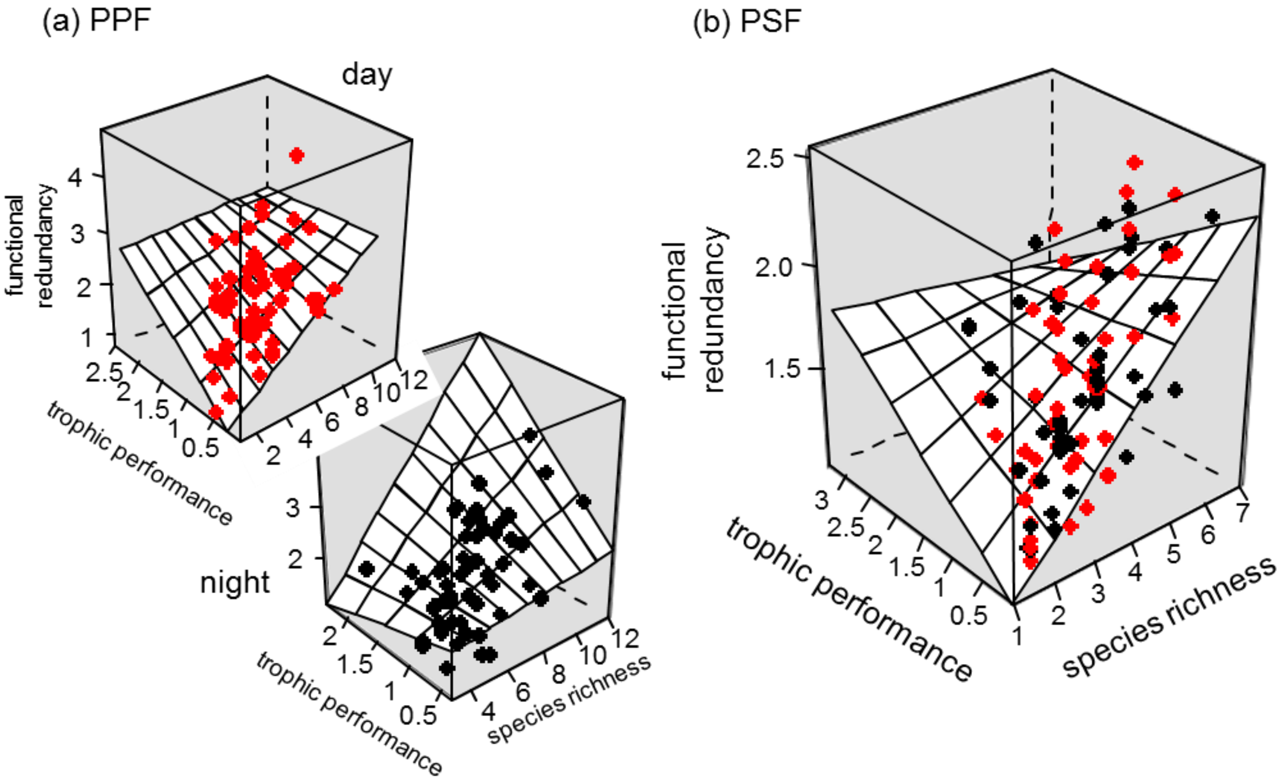
Presumably due to the low species richness per grid point and the nearly ubiquitous high performing species, functional redundancy was lowest in PSF (Fig. 1b, Table S1). In NSF, functional redundancy was highest, with the NPF and PPF in between NSF and PSF (Fig. 1b). Note that, for each grid point, FR was based on the $sTP_{i,\alpha}$ values of all species captured at the grid point using baits or pitfalls. Thus, we avoided potential bias in FR assessment due to competitive exclusion at baits. In the two neotropical forests, species richness and functional redundancy were higher during the day than at night. This was not the case in the two paleotropical forests, where species richness and functional redundancy did not differ between day and night (Fig. 1a, 1b, Table S2). In the same line, circadian asynchrony in the two neotropical sites was higher than in paleotropics (Fig. 1c). Circadian gain in functional redundancy (ΔFR) was highest in the two neotropical sites, intermediate in PPF and lowest in the PSF (Fig. 1d).

Table 1. Effects of species richness, trophic performance (TP), and time of day on FR, analyzed for each site separately using a linear mixed-effect model. All variables have 1 df. Significant *P* values are denoted with asterisks (*p < 0.05; **p < 0.01; ***p < 0.001). See Table S1 for separate day/night analyses. The abbreviations stand for 'neotropical/paleotropical,primary/secondary forest'.

Site	Factor	χ^2	*P*	
PPF	Richness	136.05	<0.0001	***
	TP	7.42	0.0065	**
	Time	0.016	0.90	
	Richness:TP	0.12	0.73	
	Richness:Time	0.58	0.45	
	TP:Time	2.50	0.11	
	Richness:TP:Time	14.00	0.00018	***
PSF	Richness	94.97	<0.0001	***
	TP	1.72	0.19	
	Time	6.06	0.014	*
	Richness:TP	8.68	0.0032	**
NPF	Richness	446.95	<0.0001	***
	TP	47.23	<0.0001	***
	Time	1.52	0.22	
	Richness:Time	4.02	0.045	*
	TP:Time	4.61	0.032	*
NSF	Richness	156.96	<0.0001	***
	TP	0.03	0.87	
	Time	7.14	0.0008	**
	Richness:TP	4.44	0.035	*
	TP:Time	6.72	0.0095	**

Functional redundancy - impacts of species richness, trophic performance and time of day

In all four sites, species richness had by far the greatest effect on functional redundancy (Table 1, Fig. 3). The effect was always positive, strongest in NPF and weakest in PSF (Table 1). Time of day influenced functional redundancy directly and via interactions. In addition to the above-mentioned species richness differences between day and night, functional redundancy was lower during the night even for equal species richness and trophic performance in NSF and PSF (significant 'time' effect; Table 1). Moreover, the positive effect of species richness on functional redundancy in NPF was weaker at night than during the day (richness:time interaction, Table 1, S4).



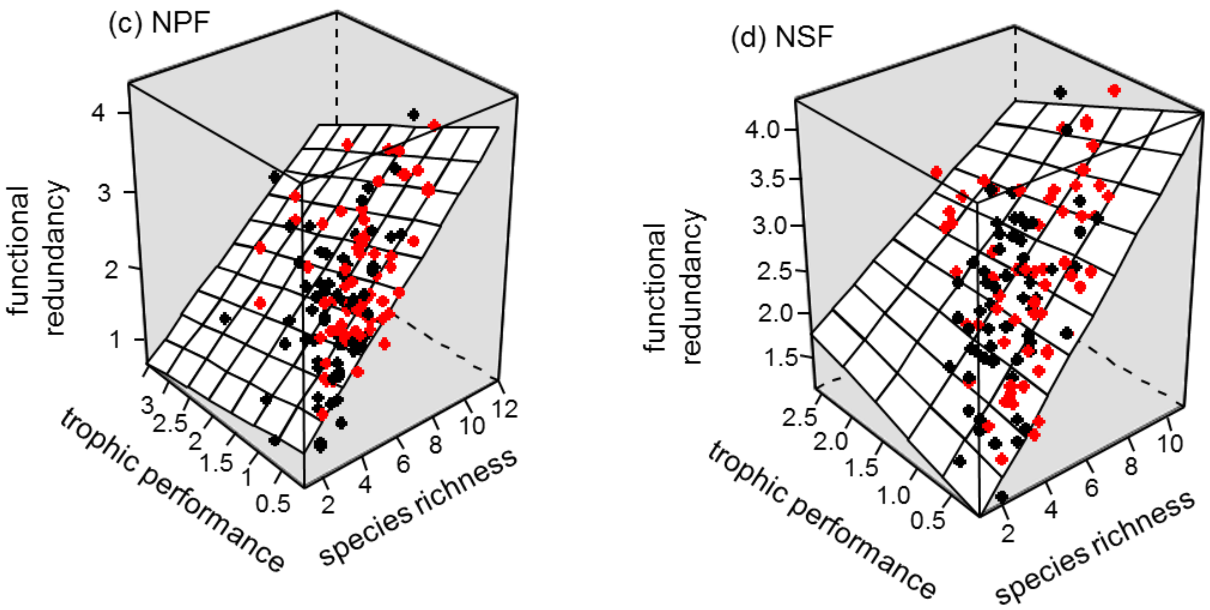


Fig. 3 Functional redundancy plotted against trophic performance and species richness in (a) PPF, separately for day and night, (b) PSF, (c) NPF and (d) NSF. The graphs show values for day (red) and night (black) as well as regression planes calculated with linear mixed-effects models. In PPF, diurnal and nocturnal communities were analyzed separately due to a 3-way interaction of time, trophic performance and species richness (Table 1).

Interactive effects of trophic performance and species richness on functional redundancy

Effects of trophic performance on FR varied between sites and times of day. In NPF, functional redundancy invariably decreased with trophic performance, but the effect was stronger at night. In NSF, trophic performance positively affected FR, but only in nocturnal communities (TP:time interactions Table 1, S4; Fig. 3). Except for NPF, effects of trophic performance interacted with species richness. At low richness levels, trophic performance enhanced functional redundancy, but, for higher species richness, this effect became weaker (in NSF and diurnal PPF) or even negative (in PSF) with higher values of overall trophic performance (Fig. 3, Fig. S2). However, in nocturnal communities in PPF, the effect of trophic performance on functional redundancy became more positive at high species richness levels (Fig. 3), which explains the three-way interaction of species richness, trophic performance and time (Table 1). Overall, the effect size of species richness on FR was negatively correlated to the relative trophic performance contribution of the high-performing species (Spearman's $\rho = -0.88$; $p = 0.0072$; Fig. 4a). The species richness effect was low in PPF and PSF, where the most frequent species was a temporally unspecialized, ubiquitous high performer. It was strongest in

NPF, where the high performer was not the most common species (NPF; Fig. S3). In diurnal NSF, the richness effect was low although the high performer was a night specialist and contributed less during the day. Presumably, this was due to additional, high performing species during day time (Fig. 2).

Table 2. Effects of species richness, circadian asynchrony and overall trophic performance (during day and night, TP) on circadian gain in functional redundancy (Δ^iFR) for each site, analyzed with a linear model. All variables have 1 df. Significant *P* values are denoted with asterisks (*p < 0.05; **p < 0.01; ***p < 0.001). The abbreviations stand for 'neotropical/paleotropical primary/secondary forest'.

Site	Factor	F	*P*	
PPF	Richness	8.89	0.0041	**
	Asynchrony	20.08	<0.0001	***
	TP	1.83	0.18	
PSF	Richness	9.71	0.0029	**
	Asynchrony	3.06	0.086	
	TP	0.02	0.90	
	TP:Richness	5.17	0.027	*
NPF	Richness	14.67	0.0003	***
	Asynchrony	5.61	0.0211	*
	TP	7.81	0.0070	**
NSF	Richness	26.91	<0.0001	***
	Asynchrony	31.84	<0.0001	***
	TP	1.90	0.17	

Circadian gain in multifunctional redundancy: ΔFR

Both species richness and asynchrony enhanced ΔFR in all sites except PSF, where the effect of asynchrony was marginal (Table 2). Compared to the effect of species richness on FR, its effect on ΔFR was much lower, and comparable to effects of asynchrony (Tables 1, 2). Trophic performance reduced ΔFR in NPF, but had no effect in PPF and NSF. In PSF, trophic performance had a negative effect on ΔFR at low levels of species richness, but a positive effect at high richness levels (Table 2, Fig. S2). Notably, circadian FR was similar in NPF and PPF despite different ΔFR and circadian asynchrony (Fig. 1b).

Discussion

Functional asynchrony is seen as an important aspect of ecosystem stability (Loreau 2010). To date, research on temporal asynchrony focused on large scales: asynchrony over seasons, years and even decades (Isbell and Loreau 2013). However, to fully understand the role of temporal asynchrony for functional redundancy and the diversity-stability relationship, as for the spatial dimension (Wang and Loreau 2014), it is necessary to investigate its role across contrasting temporal scales, including circadian cycles (Levin 1992, Whittaker et al. 2001). Across our four study sites, we found highly variable effects of species richness, asynchrony and time of day on functional redundancy. Species richness always enhanced redundancy, but its effect size was lowered if highly efficient species were frequent in space and time. Subsequently, the level of functional asynchrony between night and day was of high importance for circadian stability. Finally, the interaction effect of trophic performance and species richness on functional redundancy could be explained by the sampling effect, but was specific to certain sites and/or time frames.

Circadian asynchrony, high performing species and their effect on functional redundancy

High species turnover between day and night is common in many taxa (Fellers 1989, Andresen 2002, Devoto et al. 2011, Harvey et al. 2012), but their implications to ecosystem functioning have been barely studied till now. Here we showed that circadian asynchrony was important in the two neotropical sites, but not in the paleotropical ones. Communities characterized by high circadian asynchrony should have a higher ΔFR, and hence a relatively higher circadian redundancy, than those where nocturnal and diurnal communities are similar. Indeed, ΔFR largely corresponded to circadian asynchrony across tropical regions, with both metrics being higher in the neotropics than in the paleotropics. However, these differences between sites were not always reflected in circadian functional redundancy (e.g. between PPF and NPF), indicating that other factors can overrule this effect.

Circadian asynchrony is influenced by the temporal breadth of the ant species involved, especially the high performers. Spatial and temporal ubiquity of a high performing species (as in PSF) will result in low circadian asynchrony. In contrast, temporal specialization of the high performer (as in NSF) will be detrimental for the functional redundancy at the concerning daytime, but beneficial for circadian asynchrony and □FR. This highlights how traits such as temporal specialization of highly common and highly efficient species can affect ecosystem-level properties. Whether the traits of dominant species are similar or dissimilar to the remaining community (Grime 1998, Hillebrand *et al.* 2008), will have considerable consequences on circadian FR. Hence, studying only one time period may be as misleading as studying only one ecosystem function when investigating the diversity-stability relationship (Byrnes et al. 2014)

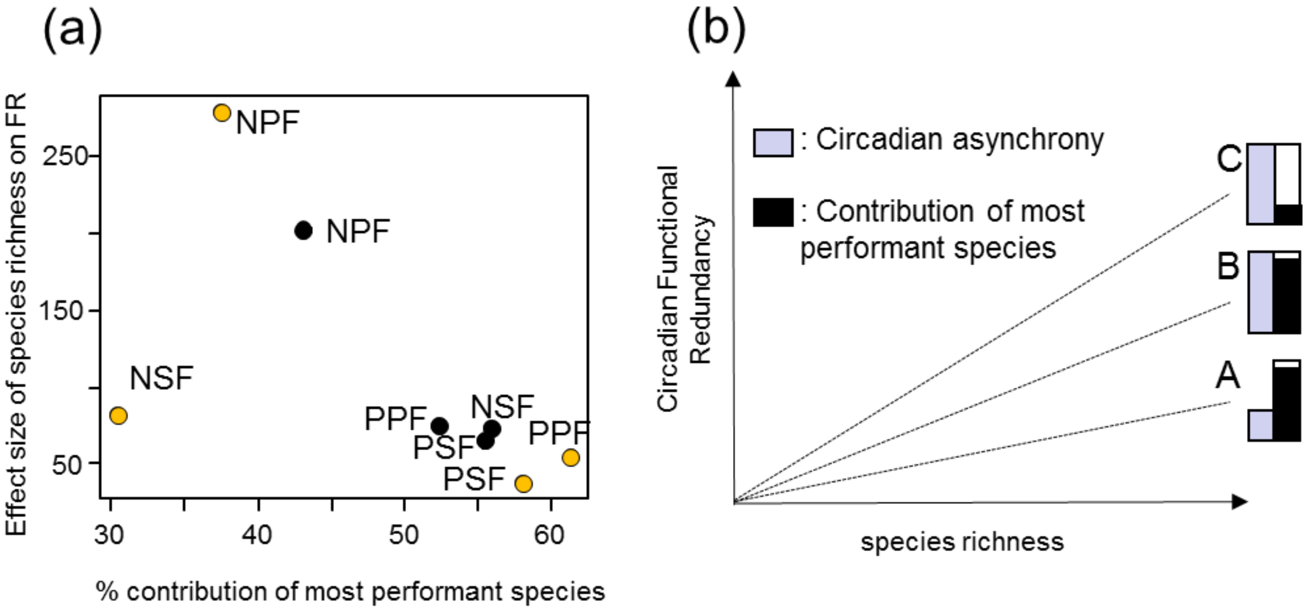


Fig.4 (a) Effect size of species richness on diurnal or nocturnal FR in relation to the relative contribution (in %) of the most performant species TP. Each data point represents the effect size (Table S4) of a site during day (yellow) or night (black).

(b) Effects of species richness, circadian asynchrony and the contribution of a high-performer on circadian functional redundancy. Grey bars (left) represent high or low levels of circadian asynchrony. The right-hand bar shows the percent contribution of the highest-performing species to overall trophic performance; the slope of the regression lines represents the effect size of species richness on circadian functional redundancy. We define 3 major scenarios:

(A) Low circadian asynchrony, and trophic performance mostly done by a single, high-performing species results in the weakest effect of species richness on FR (PSF, PPF).

(B) High circadian asynchrony, and trophic performance mostly done by a single, high-performing species results in a stronger effect of species richness on FR (comparable to NSF).

(C) High circadian asynchrony, and low relative contribution of the high-performing species results in the strongest effect of species richness on FR (NPF).

Effects of high trophic performance and species richness on functional redundancy

Species richness has been seen as a good predictor of stability (de Mazancourt et al. 2013) and a useful surrogate of functional diversity (Bihn et al. 2010). We evaluated the generality of this hypothesis by studying forests of different biogeographic region and disturbance status. Indeed, species richness always enhanced functional redundancy in our data. Nevertheless, effect sizes were highly variable. For sites with similar mean species richness, different levels of FR were obtained (e.g. in NPF and NSF), probably because the high performing species differed in commonness and temporal breadth across sites (Fig. 4b).

In three of four sites, grid points where a high performing species was present had a significantly higher trophic performance than gridpoints where it was absent. This suggests that high levels of trophic performance can only be achieved through the presence of few, highly efficient species, but not by even contributions of several, less efficient ones. These data corroborate a recent meta-analysis, where performance of polycultures was similar, but not higher than performance of monocultures of the single, most efficient species (Cardinale et al. 2006). Highly efficient species, however, make the function they perform vulnerable to species loss, since their extinction is harder to buffer by the other species. If high performance on a grid point is invariably due to the presence of highly efficient species (such as in NPF), trophic performance will have a negative effect on functional redundancy due to the uneven functional contributions of the species involved (Fig. S1a). In the other sites, trophic performance positively influenced functional redundancy at low levels of species richness, but at high species richness, this effect became weaker (NSF, diurnal PPF) or even negative (PSF). In our opinion, this can be explained by the sampling effect (Cardinale et al. 2006): at high levels of species richness, there is a higher likelihood of obtaining highly efficient species, which increase trophic performance but reduce functional redundancy. In PSF, the TP:richness interaction suggested that the sampling effect was strongest, although a high-performer was nearly ubiquitous at this site. Grid points with high species richness at PSF brought forward species with even higher performance than the overall high performer (Fig. 2, S1b). Thus, we suggest that the sampling effect is genuine and occurs in biological communities, but is specific to certain community assemblages and time frames.

Conclusions

By assessing multiple ecosystem functions during day and night across varying habitats, we showed that functional redundancy can differ between day and night, and circadian asynchrony can greatly influence the circadian gain in functional redundancy. Diurnal and nocturnal ecosystem properties of the very same habitat can markedly differ in terms of species richness, functional redundancy and the presence of high performers. Our study thus highlights that the importance of studying multiple time periods in order to understand the diversity-stability relationship.

We showed that the influence of species richness on functional redundancy depends on the relative functional contribution of the most efficient species, which in turn is affected by its spatial frequency and temporal breadth. High trophic performance was generally due to few, highly efficient species, but rarely to even contributions of less efficient ones. We suggest that circadian asynchrony and the functional contribution of efficient species jointly influence the effect of species richness on circadian functional redundancy (Fig. 4).

The two tropical regions differed markedly in terms of asynchrony, and the forest condition (secondary/primary) was no clear indicator of its level of functional redundancy. Moreover, the ‘sampling effect' was specific to certain sites and/or time frames. Hence, generalizations across varying community assemblages are hard to apply. Site differences may be caused by frequency and temporal specialization of high performers, but also by other factors such as spatial heterogeneity or the degree of competitive exclusion.

Compared to larger-scale experiments, fine-scale studies provide limited predictability of an ecosystem, but may enable to pinpoint more vulnerable habitats (with lower asynchrony or lower redundancy) without the logistical constraints of long-term experiments. By analysing asynchrony through a finer scale, we hope to contribute towards building a broader framework helpful for conservation purposes.

General Discussion

An extensive body of research has focused on the biodiversity ecosystem functioning (BEF) relation of primary producers, where the ecosystem provides valuable economical services (Balvanera et al. 2006, Isbell et al. 2011, Schneiders et al. 2012). In order to understand the mechanisms of coexistence in higher trophic levels and how it relates to the (BEF) relation between species, researchers have inferred functional aspects from life history traits, morphological characteristics and isotope analysis. As we have argued previously, if this was an important first step, it nonetheless represented a crude measure of the relation between traits and functional performance. By analysing the contribution of different species to a given ecosystem function (our reversed approach), we may be limiting the number of trophic functions we might encompass. But the relation between the species of a community and each trophic function was empirically crystal clear and enabled us to provide the Trophic Performance index (TP) found in chapter 3. This index was insightful in enabling us to quantify the relative contribution of different species to a given ecosystem function and measure accurately the stability of an ecosystem through functional redundancy.

Trophic Performance

Among the elements integrated in this index, two deserve particular attention. Firstly, assessing each species' capacity to consume resources can be regarded as a measure of functional performance, analogous to primary production in plants. It was estimated, according to the metabolic theory, that the resource quantity consumed by any animal, i.e. its consumption rate, is proportional to the $3/4^{th}$ power of its biomass M (Allen et al. 2002) for a given set of temperatures and taxa; the theory is sound but challenging with regard to polymorphism in ant species (Morrison 2000). With dimorphic species (major and minor), an average ratio may be calculated if enough recruitment on each bait has been quantified. However, for polymorphic species (major, media, minor), the range of different sizes disables a possible ratio (but see Bihn et al., 2010), and only an average biomass may be estimated over a vast number of weighed recruitments. Firstly this implies an even distribution of different casts within and out of a colony. Secondly determining the relative abundance of a given species for a specific resource is a problematic issue. Whatever the mathematical tool (mean, weighted mean, median), several ecological factors may influence these values with nest proximity being the most problematic.

Therefore species abundances and frequencies need to be corrected by taking in consideration the spatial distribution of species. Even though pitfall traps may be slightly biased towards species that fall into traps more readily than others (Stuble et al. 2013). To my knowledge they represent the only base line to correct for relative frequencies of the species actively foraging on the surface, and have also been used in relation to baits to define ecologically dominant species (Andersen 1992).

Baiting method

The baiting method established during my PhD is pioneer in quantifying the BEF relationship in invertebrates and therefore needs to be thoroughly discussed. The advantages of traditional cafeteria experiments with monitoring are that it enables us to assess functional traits such as preferred food and segregation behaviour (Dejean et al. 1999, Sanders and Gordon 2003, Menzel et al. 2012). Even though presenting several baits simultaneously does allow us to define a species preferred food, this approach fails to provide information of what a species may forage besides its preferred food. Moreover, this type of sampling is limited in the number of replicates one can observe simultaneously. Additionally, the identification and quantification by observation of morphospecies may be hazardous in certain hyper diverse genera (e.g. *Pheidole, Solenopsis)*, particularly at night. The method of sampling we devised using retrieval boxes was conceived to exploit the advantages of cafeteria experiments while reducing the limitations related to monitoring. The absence of monitoring on baits enabled us to increase the number of samples left out (32 per usual sampling session and 1024 in total per site) and retrieving the ants for a more accurate quantification. We expected that the information usually gathered by monitoring would be instead gained by the sheer number of replicates. Our method did indeed enable the demonstration of segregation capacities, temporal and dietary preferences. Our results also revealed that previous measures may have overlooked important aspects. For instance, several of the specialised predatory species we sampled were found predating but also scavenging (*odontomachus, pachycondyla*), which would not have been detected through isotope analysis. Another predatory species *(myoponera, unpublished data)* was found frequently feeding on carbohydrates, a finding which we would not expect based on morphological traits.

Combining passive and active sampling, such as the data of pitfall and bait sampling (Andersen 1992, Andersen and Patel 1994, Sanders and Gordon 2003, Stuble et al. 2011, Baccaro et al. 2012), provides a more thorough assessment of a species abundance and spatial distribution and valuable information on the success rate of our baiting method. Indeed, an issue arose concerning big predatory species that seldom recruits. Even though live baits were displayed in a manner that was thought to slow down prey removal, solitary predatory ants' frequencies on baits (e.g *Pachycondyla, Odontomachus*) were undermined in comparison to their pitfall frequency. It would, therefore, appear that the display needs improving or that monitoring is still required for live baits. Species on other baits were not undermined, but certain points are nonetheless worth mentioning. Liquid baits such as carbohydrates must be carefully displayed in relation to the environmental conditions. Depending on sugar concentration, temperature and humidity the liquid solutions may evaporate sooner or later (during the 90 min display) which may alter its level of attractiveness. Oleic acid was initially thought to be an interesting attractant in relation to elaiosome seeds (Reifenrath et al. 2012), which would enable us to distinguish between ant functioning as seed dispersers or granivores. However, this oily substance is also found in decaying insects and may have simply attracted ants due to its lipid rich content; additionally, we lacked the botanical information about the presence or not of elaiosome plants, which made this bait difficult to define as a trophic function for specific ecosystems.

Mechanisms of coexistence in relation to niche plasticity

The first chapter of this thesis demonstrates that temporal and dietary differences may be found on community as well as on species level.

Community compositions were clearly different at night or day, which concords with previous findings where temporal partitioning was the most relevant (among the trade-offs tested) aspect of coexistence between species of a same community (Fellers 1989, Albrecht and Gotelli 2001, Stuble et al. 2011). Based on the multifunctional approach of this thesis, we were able to go a step further and also analyse resource partitioning through a range of complementary baits. Even though a number of clear differences were found between certain resources, some types of baits were similar in the communities that they attracted (Chapter 1). Even though certain species were present on only one of these resources, the bulk of the recruitments were performed by analogous ants, thus rendering them similar on a community level. It is therefore interesting to look at each species separately to further understand the relation between niche specialisation and coexistence.

Species frequently presented temporal and food preferences, but they seldom displayed strict temporal or dietary exclusiveness. In chapter 1 we saw that certain species showed differing temporal preferences (but never opposite) depending on the sampling method. These facts suggest that species-realized niche traits may display a certain level of flexibility in relation to their fundamental niche. Niche plasticity may enable species to coexist via niche pre-emption where species may respond to the presence of a superior competitor by switching to an alternative, less used resource (Sanders and Gordon 2003, Ashton et al. 2010). These levels of trait flexibility are of growing concern both in plant and animal ecology (Heemsbergen et al. 2004) as functional traits may vary as much within as between species (Valladares and Niinemets 2008) and, in consequence, impair the explanatory power of trait-based analyses in predictive models (Berg and Ellers 2010). Hence, the question remains whether fixed traits can be generalized for a species with no consideration for the ecological context (Messier et al. 2010). This thesis demonstrated that temporal and dietary preferences may significantly differ between sites (chapter 2), to the extent that certain species niches may be closer to other species than conspecifics, and that the level of plasticity is dependent on the dominance hierarchy established in a community, which is, in turn, dependent on the ecological context. Hence ecological indices which base diversity on morphological characteristics or life history traits (Ilg and Foeckler 2012, Demars et al. 2012, Sternberg and Kennard 2014, Mlambo 2014) must take into consideration the trait plasticity of a species in relation to its ecological context. Especially since these are precisely the type of traits that are highly plastic in response to environmental change (Roff et al. 2002). The different levels of plasticity among species (and within species) convey differences in realized niches that emphasize the functional asynchrony of species, an essential aspect of ecosystem stability (Loreau 2010). This is a vital feature of our understanding of stability and how species within a community may respond to perturbations such as habitat disturbance or climate change. Once again our current knowledge is mostly focused on the response diversity of plants (Laliberté et al. 2010) while little is still known for higher trophic levels. Chapter 2 is only a first step in bridging this gap.

Ecosystem stability

Climate change and other human-driven (anthropogenic) environmental changes will continue to cause biodiversity loss in the coming decades (Sala et al. 2000), in addition to the high rates of species extinctions already occurring worldwide (Stork 2009). It is therefore essential to clearly understand the mechanisms that promote stability in relation to biodiversity. For instance if the populations of different species fluctuate asynchronously through time, the sum of their populations, and thereby their total functional contributions, varies less over time than that of any single species, which enhances stability (Doak et al. 1998, Yachi and Loreau 1999, Garibaldi et al. 2011). While this is true in principle, this assertion does not take into consideration the ecosystem performance of different species. Whether the traits of dominant species are similar or dissimilar to the remaining community (Grime 1998, Hillebrand *et al.* 2008), will have considerable consequences on the asynchronous population fluctuation. In chapter 3 we demonstrate that most high levels of trophic performance can only be achieved through the presence of few, highly efficient species, and not by even contributions of several, less efficient ones. Hence stability through asynchrony depends on the even functional performance of different species and their temporal asynchrony in a given community.

Most work considering temporal asynchrony was conducted on plants, for which seasonal and inter-annual changes are most important (Isbell et al. 2011), while few studies have investigated the role of circadian cycles for ecosystem functioning (but see Andresen 2002, Boulay et al. 2007). Chapter 3 demonstrates that diurnal and nocturnal ecosystem properties of the very same habitat can markedly differ in terms of species richness, functional redundancy and the presence of high performers. Hence even short term functional asynchrony may influence the stability of an ecosystem and needs to be considered in predictive models.

Future Research: expanding the niche concept

The two main aspects of this thesis, mechanisms of coexistence and ecosystem stability, are governed by similar aspects where, in general, the conditions that promote species coexistence within communities also promote the long term stabilizing effect of biodiversity on ecosystem functioning. These aspects are intertwined and limited by our lack of predictive ability (especially in animals) in forecasting how a species niche adapts to its environment (on short evolutionary scales).

Fundamental and realized niche is an everlasting dilemma in ecology, in order to understand the capacity of a species to restrict its niche (realized) one must be able to define its fundamental niche. However, certain researchers consider this fundamental niche as a hypothetical concept (Malanson 1997), which is visualized as being the niche in the absence of competitors or biotic conditions that may affect the species persistence over time. Defining the fundamental niche for different species would require determining the growth rate (r) of a species under the n

parameters defining its environmental conditions (humidity, food, temperature, strata…), until one finds the optimum *r* through all possible combinations of the different *n* parameters (in all the ranges of each parameter).

If this is theoretically plausible, in reality it is unfeasible. As a consequence, fundamental niches are rarely measured and we do not know when or if realized niches are narrower than fundamental niches as a result of competition, or if the realized niches can be wider owing to the sink out effect (Pulliam 1988), where species may occur but not thrive. This fundamental–realized niche framework begins with clearly understanding the drivers of a species niche. This thesis focused mostly on biotic factors that may govern niche plasticity, which enabled us to better understand complexity of niche partitioning. Future research should, in a first step, define a framework combining main biotic and abiotic factors that govern a species-specific niche. Depending on the complexity of the ecosystem, micro habitat variation will be the most challenging and novel aspect. In this regard quantifying resource limitation/availability such as in carbohydrates or nitrogen resources might be near impossible in complex habitats. An alternative strategy would be to control these limitations by artificially providing one resource constantly which would enable its removal as a possible limiting factor. In a second more empirical step, it is necessary to gather data on these factors that govern the realized niche of a given species in a similar manner than the one described in chapter 3, and then replicate this on a scale which is relevant to the species natural geographical range. The success of a realized niche would be defined by the relative biomass of a species for a given set of biotic and abiotic conditions. In a final modelling step, inspired by the NICHE model (Pulliam 2000) and this thesis, it is necessary to use the biotic and abiotic data collected as explanatory variables of the species success in different realized niche. This would enable us to see, first of all, which factors are the most influential in a given species niche and, second, to see how the fluctuation of these different factors influences the realized niche in order to realistically predict the fundamental niche of a species. The capacity to define a species fundamental niche boundaries based on biotic and abiotic factors would be a tremendous achievement (especially for invertebrates) in our capacity to predict a species' (or a community's) response to environmental change.

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Appendix section

Supplement chapter 1

S1: Sampling design

We established four plots of 4 x 4 grid points each (16 points per square plot), i.e. a total number of 64 grid points. The grid points in the plots were separated by 10 m each all plots were less than 100 m from one another. At each grid point, we presented in total eight different baits, both during day and at night, and placed pitfalls during day and at night. However, to avoid interference between multiple baits, only one bait or one pitfall was presented at each grid point at a given time. We took care that, during each sampling session, all eight baits were presented evenly (at different grid points), in order to avoid any bias due to fluctuating weather conditions. Pitfalls were only placed when no baiting was performed on the same plot.

All ants collected were preserved in 75% ethanol. They were counted and sorted to morphospecies by Mickal Houadria and Alex Salas-Lopez, based on Bolton (1997). Voucher specimens of all species are deposited at the Institute of Zoology, University of Mainz.

Pitfalls

The pitfall traps (Ø 4cm, depth 6cm) were buried in level with the surrounding soil surface and replaced after each sampling session (into the same hole) to reduce the digging-in effect (Greenslade 1973). They were opened for 10 hours between 20h30 to 6h30 for the nocturnal traps and between 7h00 to 17h00 for the diurnal ones. For each grid point, we obtained three 10-hour replicates day and night, yielding a total of 60 sampling hours. To kill and preserve the ants, the traps were filled ca. 1.5 cm high with a 50% propylene glycol solution. This preservative is non-toxic to vertebrates at these quantities and neither attracts nor repels ants (Boonzaaier et al. 2007).

Displaying the bait

The boxes were placed 1 cm deep in the ground and had, 6 mm above the bottom, two slit-like openings (1 cm wide and 8 cm long), level with the ground. They could be quickly retrieved by encasing into a similar box without side openings. As plastic is potentially avoided by some ants, the base of the box were covered with paper towel. A hole in the lid allowed squirting the killing solution (propylene glycol solution 70%) right after retrieval.

The liquid solutions were pipetted directly onto the paper towel in the baiting device while the solid baits were put into the centre of the devices. Live baits were harder to display. Approximately ten termites were maintained free on the paper towel and usually stayed at a small piece of termite mound which was added. To avoid that all termites would be captured before the end of the sampling approximately five further individuals were glued live on a 2 cm stick with odourless rat glue (Greenleaf Ltd., Beijing, China). For grasshoppers, in order to partly maintain their ability to jump but restrain it to the baiting device, we tethered it to a fine, 3 cm long string which was pinned to the base of the boxes.

The baits were presented for 90min during the day (between 10h00 and 15h00) and at night (between 20h00 and 23h00). Preliminary tests had shown that this time was sufficient to allow at least partial recruitment on all baits, but was not long enough to have dominant ants saturating the majority of the most attractive baits.

S2: Pair wise similarities between different baits

Ant communities at sucrose (a disaccharide) did not differ from those at melezitose, which is a trisaccharide common in honeydew (Völkl et al. 1999). Hence, the regular consumption of melezitose-containing honeydew may not represent an option to evade competition by sucrose-foraging species. Furthermore, we had expected to find different predatory ant species at grasshoppers and termites. Apparently, the same ant species could overwhelm the two prey items regardless of their size.

Many ant predators are solitary foragers, specialised on certain prey types, do not recruit, and immediately retrieve the whole food item to their nest instead of feeding directly at the spot (Dornhaus and Powell 2010). Thus, the chances of capturing such species without constant bait observation are smaller compared to species that recruit massively and do not retrieve large pieces of bait. *Pachycondyla crassinoda* for instance was only found twice on crickets and once on crushed insects but had a high pitfall incidence (Fig. 2). Therefore presenting suitable live prey species in an appropriate manner may prove difficult and may partly explain the similarities found between termites ands grasshoppers. For future studies, the set of baits should be continuously extended or amended with complementary baits and/or specific displays, aiming to cover as many species as possible.

We had not expected seeds and elaiosome to be similar as the latter is assumed to contain oleic acid as attractant (Boulay et al. 2005, Bronstein et al. 2006), but see (Reifenrath et al. 2012), and the presence of a chemical food cue alone often suffices to attract specialised species (Schmitt et al. 2004). However, no information could be obtained on the diversity of elaiosome-bearing plants at the site

Supplement chapter 2

Table S1: Euclidean distances between species niches in the two sites. Bold numbers give the difference for conspecific niche distances. “CN > IN” corresponds to the number of species which have a lower niche distance to the species in question (interspecific niche distance, IN) than to its conspecific (CN).

		Malua								
	Species	Cam sp.1	Eup sp.1	Lop sp.1	Lop sp.2	Phe sp.6	Car sp.1	Rec sp.2	Tec sp.2	*CN>IN (Malua)*
Danum	Cam sp.1	**30.2**	46.1	27.5	25.9	40.4	30.4	34	37.5	2
	Eup sp.1	47.7	**38**	22.1	33.8	37	19.9	26.5	20.2	6
	Lop sp.1	33.4	41.1	**7.6**	14.1	32.7	17.8	17.5	25.3	0
	Lop sp.2	30.2	52.7	17.3	**17.5**	37.7	20.7	18.9	31.8	1
	Phe sp.6	46.3	42.5	23.2	33	**34.6**	18.6	29.8	25.3	5
	Car sp.1	37.9	39.3	21.3	28.5	28.6	**15.7**	30.5	26.8	0
	Rec sp.2	41.9	53.3	28.2	33.4	43.3	24.1	**20.4**	35.9	0
	Tec sp.2	65.1	37.8	40.9	49.8	60.6	47.3	46.2	**33**	0
	CN>IN (Danum)	1	1	0	1	2	0	2	5	

Supplement chapter 3

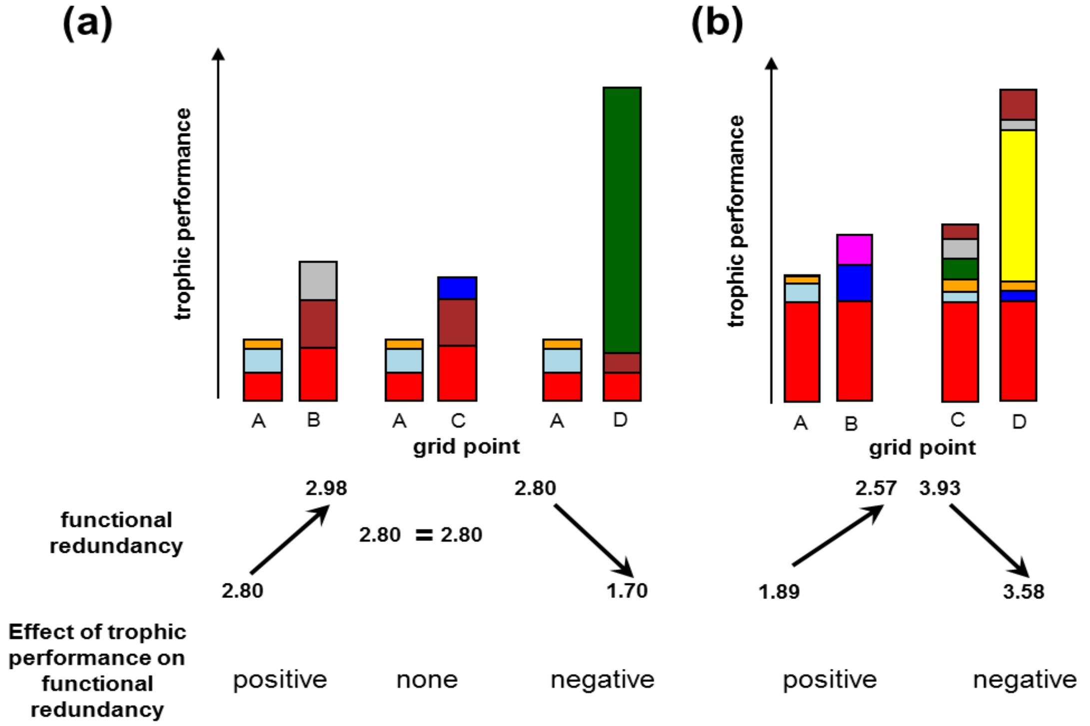

Fig. S1 Relation between trophic performance, functional redundancy (FR), and the sampling effect. Each bar represents a grid point, on which several species (colours) contribute to overall trophic performance. All presented FR values are based on calculations of the depicted, hypothetical trophic performance values (hence, no units are given).

(a) On the grid points B vs. A and C vs. A, higher trophic performance is due to higher, but relatively even contributions of each species. Hence, FR remains constant or increases with trophic performance. On grid point D, higher trophic performance is largely due to a single high performer. Hence, FR decreases with trophic performance. The effect of trophic performance on FR at a constant species richness allow to evaluate the evenness of the species-wise functional contributions. In our study, very high performance was often achieved by a high performer, but rarely by even contributions of multiple low performers.

(b) In site such as PSF (Malua), high performers are ubiquitous. Hence, FR is low due to uneven species contributions. At low species richness (A and B; 3 species each), FR increases with trophic performance since the evenness of functional contributions increases. At higher species richness (C and D; 5 species each), the likelihood of a second high performer increases. Hence, grid points with high trophic performance can have a lower FR (D vs. C).

The sampling effect occurs if an increase in performance with species richness is due to a single, highly efficient species rather than multiple equally performing species. Here, this is detectable in that trophic performance *negatively* affects functional redundancy at high species richness. Given a positive effect at low species richness, trophic performance and species richness will have an interaction effect on FR.

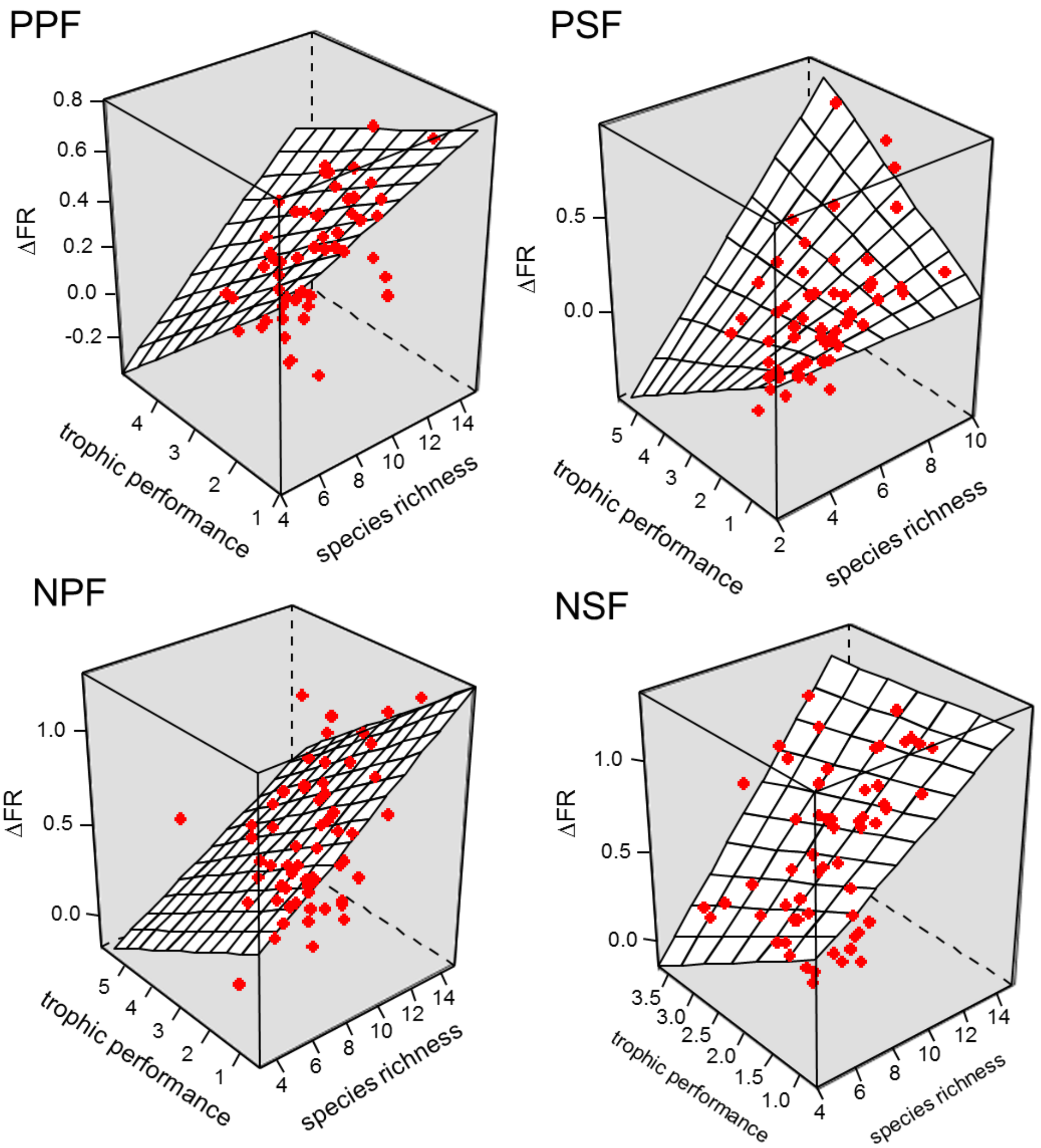

Fig. S2 ΔFR plotted against trophic performance and species richness. The graphs show original values and regression planes calculated with linear mixed-effects models.

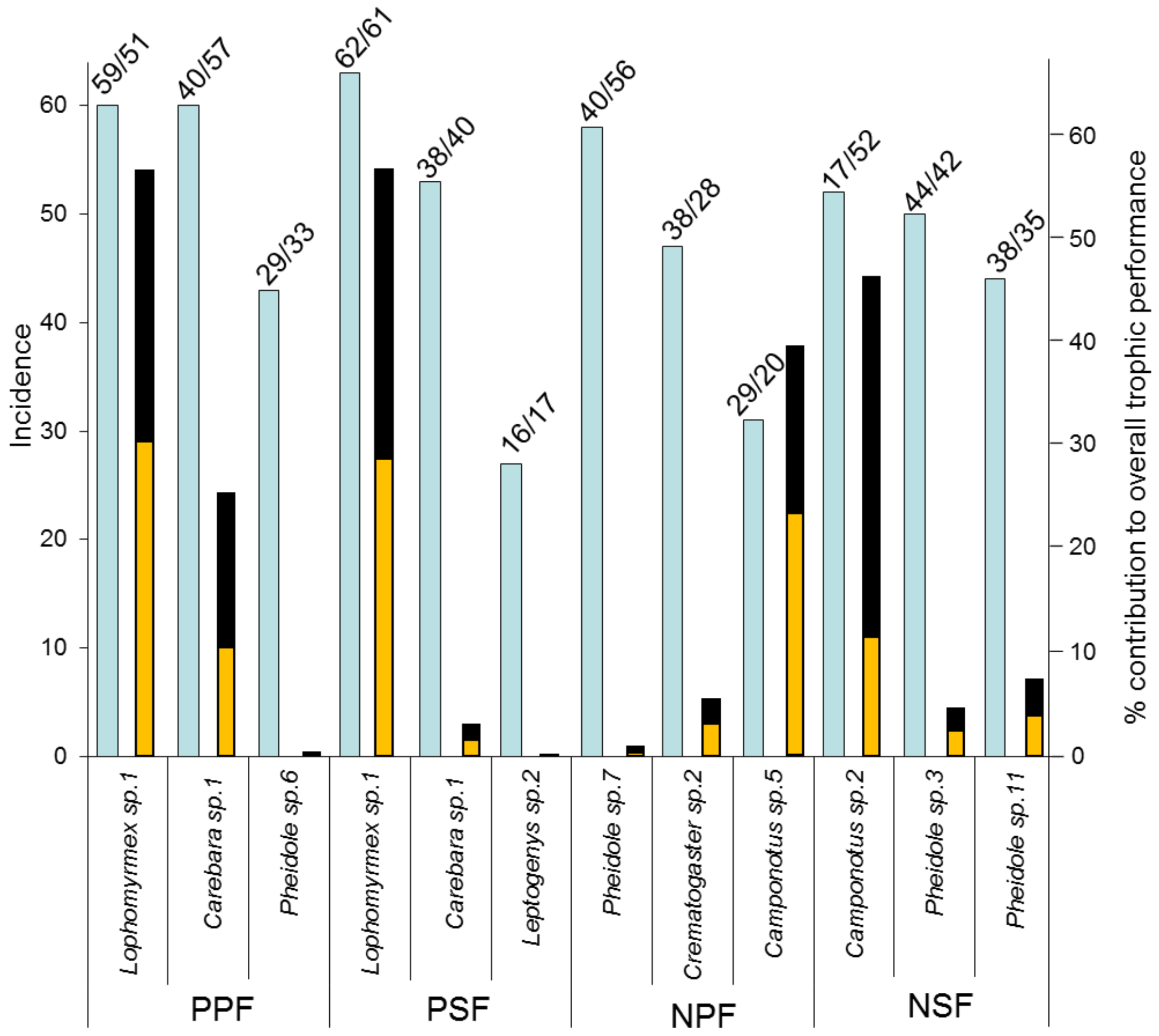

Fig. S3 For each site, the plots show incidence and relative TP contribution of the three species with highest incidence. Incidence (day and night pooled; 1-64 grid points) is shown by the blue bars. The numbers indicate incidence during day and night separately. Relative TP contribution (in %) is given by the yellow and black bars, which represent diurnal and nocturnal contribution (respectively).

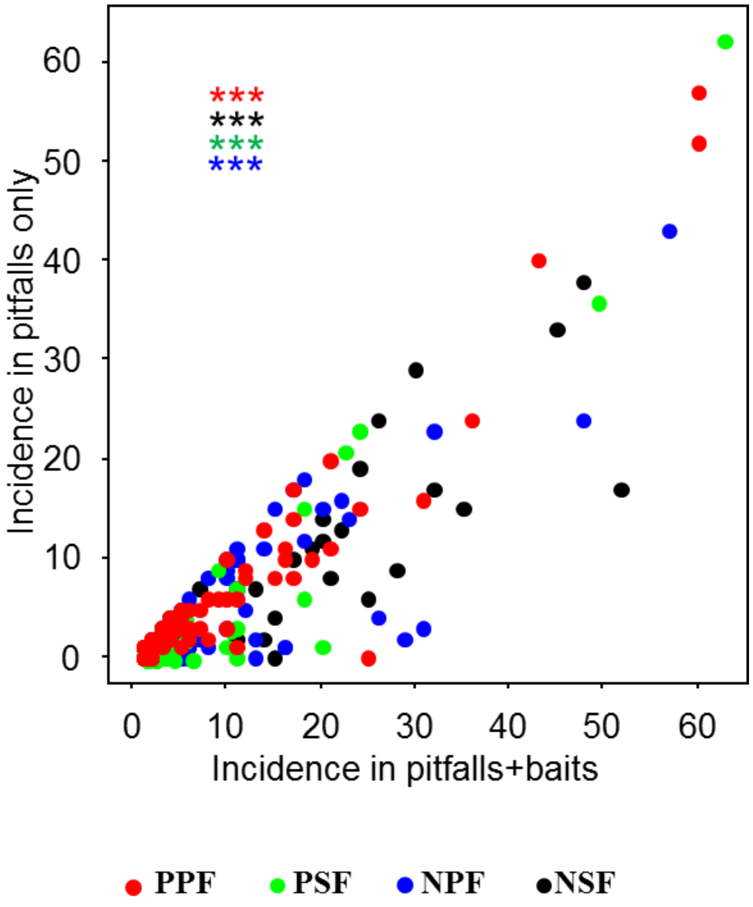

Fig. S4 Species-wise incidence on pitfalls plotted against incidence on baits and pitfalls. The two metrics are highly correlated for each site. In red PPF (Pearson correlation: t = 26.94, df = 90, r = 0.94, p < 0.0001); in green PSF (t = 25.19, df = 83, r = 0.94, p < 0.0001); in blue NPF (t = 14.95, df = 106, r = 0.82, p < 0.0001) and black NSF (t = 12.16, df = 48, r = 0.87, p < 0.0001).

Declaration

Versicherung

Für den Gesuch um Zulassung zur Promotion in den Fachbereichen 17 - 22 der Johannes Gutenberg-Universität Mainz.

Ich, Mikal Yann Isani Houadria, geboren am 13.06.1984 in Echirolles in Frankreich, versichere gemäß § 11, Abs. 3d der Promotionsordnung vom 22.12.2003, dass

- ich die heute als Dissertation vorgelegte Arbeit selbst angefertigt und alle benutzen Hilfsmittel (Literatur, Apparaturen, Material) in der Arbeit angegeben habe.
- ich die jetzt als Dissertation vorgelegte Arbeit nicht als Prüfungsarbeit für eine staatliche oder andere wissenschaftliche Prüfung eingereicht habe oder hatte.
- ich weder die jetzt als Dissertation vorgelegte Arbeit noch Teile einer Abhandlung bei einer anderen Fakultät bzw. einem anderen Fachbereich als Dissertation eingereicht hatte

Mainz, den 10.11.2014

(Mikal Yann Isani Houadria)
