The recovery of ant communities in regenerating tropical forests

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Marburg, September 2008

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1 General Introduction

Biodiversity in tropical forests

Tropical forests are the most diverse and the most ecologically complex of all terrestrial ecosystems. Though occupying only 7% of the Earth's land surface, they probably sustain over two-thirds of all species (Raven 1980; Wilson 1992) and play a disproportionately large role in global carbon and energy cycles (IPCC 2002). Human impacts, however, cause the destruction of tropical forests at an alarming rate. Originally, these forests covered between 14 million and 18 million square kilometers. Today, only about half of the original area remains (Raven 1980). Much of this reduction is recent, and clearing now eliminates about 1 million square kilometers every 5 to 10 years (Skole and Tucker 1993; Nepstad et al. 1999; Cochrane et al. 1999). Since biodiversity is so extraordinarily concentrated in tropical forests, this habitat loss is widely anticipated to lead to a mass extinction of species if current rates of deforestation continue (e.g. Pimm et al. 1995; Dirzo and Raven 2003). Even careful estimates indicate a current species extinction rate several orders of magnitude higher than historical background rates (Groombridge 1992; Regan et al. 2001). This threat to tropical forests has given rise to great international concern about the potential loss of biodiversity. The question of protecting forests under a binding convention has challenged nations like few other environmental issues and dominated much of the 1992 United Nations Conference on Environment and Development (Earth Summit) held in Rio de Janeiro.

Deforestation, however, is rarely permanent — converted land is exhausted, abandoned and allowed to regrow (Nepstadt et al. 1991; Corlett 1995). These *secondary forests* increasingly dominate the tropical wooded landscape. The majority of tropical countries today has more secondary than primary forests. In a recent review and analysis of tropical deforestation, Wright and Muller-Landau (2006) predict that natural forest regeneration via secondary succession will accelerate and eventually overtake clearing rates, resulting in a net stabilization or even increase in total forest cover. Their analysis showed that the remaining forest cover depends on human population density in rural areas. Since rural populations are supposed to decrease in the near future, net forest loss might be lower than previously expected. They conclude that „the widely anticipated mass extinction of tropical forest species will be avoided" (Wright and Muller-Landau 2006). This controversial paper generated a vigorous debate about the tropical biodiversity crisis (e.g. Brook et al. 2006; Gardner et al. 2007; Laurance 2007). One of the key assumptions of Wright and Muller-Landau is that secondary forests can sustain the same species that depend on old-growth forests. The biodiversity value of secondary forests in the tropics, however, is an area of much uncertainty and relatively little is known about faunal recovery in secondary forests, particularly of invertebrates.

In the following, I will first review the current knowledge about the biodiversity value of secondary forests (or lack thereof) using the recovery of *species diversity* of ants (Hymenoptera: Formicidae) as an example. Next, I will explore the potential consequences of the loss of *functional diversity* in secondary forests. From a human perspective, the conservation of ecosystem functions might be more important than the conservation of species diversity as such. Functional diversity is emerging as an important aspect of biodiversity as it determines the strength and shape of the relationship between species diversity and ecosystem functions. Lastly, I will consider the ecosystem changes during tropical forest succession and how they influence *community assembly*. Application of the theory of assembly rules in the context of the recovery of biodiversity in tropical secondary forests might be useful to guide future restoration and conservation projects.

Ant species diversity in tropical secondary forests

The meta-analysis by Dunn (2004) provides the only quantitative review of the value of secondary forests as habitat for tropical forest animal species and is key to the optimistic outlook of Wright and Muller-Landau. In his review, Dunn concludes that species richness of tropical faunal communities, and species richness of ants in particular, take roughly 40 years for complete recovery. Focusing on species richness alone, however, might be an insufficient indicator of the recovery of forest-adapted species. As already pointed out by Dunn, species composition recovers much more slowly and many mature-forest species can still be absent in secondary forests (Dunn 2004).

Ants are the most frequently studied taxon for the recovery of faunal diversity in tropical secondary forests (Dunn 2004). Dunn based his meta-analysis about the recovery of ant species diversity on eleven published studies of ant recovery in tropical forests. In Dunn's paper titled *"Recovery of faunal communities during tropical forest regeneration"* it is quite astonishing, that three of the analyzed studies (MacKay et al. 1991; Verhaagh 1991; Watt et al. 2002) did not sample ants in secondary forests but only in mature forests and cleared/agricultural areas. The notion that species richness and composition of ant communities differ between these contrasting habitats is well established and rather trivial. Moreover, these studies do not contribute any information on the recovery of the fauna during *forest regeneration*. In the study of Watt (Watt et al. 1997), mature forests were not even sampled. Without the inclusion of undisturbed forests as a control, it is not possible to evaluate the dynamics of faunal recovery in secondary forests. The level of replication in these studies on ant recovery in secondary forests was also very poor, and eight of the eleven studies had no replication within treatments (i.e. the studies of MacKay et al. 1991; Verhaagh 1991; Bustos and Ulloa-Chacón 1997; Lawton et al. 1998; Moutinho 1998; Estrada and Fernández 1999; Vasconcelos 1999; Watt et al. 2002). Secondary forests in the surveyed studies originated in a wide variety of ways. In some studies, secondary forests resulted from selective logging for the harvest of timber or the creation of plantations (e.g. Roth et al. 1994; Watt et al. 1997; Lawton et al. 1998). Secondary forests in other studies were regrowing after complete clearance (e.g. Belshaw and Bolton 1993; Bustos and Ulloa-Chacón 1997; Moutinho 1998). The key difference between these two types of secondary forests is the continuity of forest cover. Selective logging leads to changes in the relative proportions of each species; complete clearance eliminates most or all forest species and recovery has to start from scratch. These differences have important consequences for the speed of faunal recovery. Sampling methodologies and effort were also very different. For example, six studies used baiting for the sampling of ants (MacKay et al. 1991; Verhaagh 1991; Roth et al. 1994; Bustos and Ulloa-Chacón 1997; Estrada and Fernández 1999; Vasconcelos 1999). This sampling technique tends to capture only the most generalist species and misses species with more specialized resource requirements. Such species are often more likely to occur in more heterogenous environments (i.e. primary forests) and this sampling procedure is thus biased against revealing the true diversity of undisturbed habitats. In summary, differences in local habitat, weak sampling design, differences in land use history and poor sample representation severely limit our ability to generalize the results from the referenced studies on ant diversity recovery in secondary tropical forests. A meta-analysis does not necessarily overcome these limits.

This weak data basis for studies of faunal recovery in tropical secondary forests is not restricted to the recovery of ant communities but the situation is similar for other animal taxa (e.g. see Gardner et al. (2007) for a review of studies on birds, amphibians, reptiles and primates). There is a general lack of knowledge about the recovery of animal diversity in secondary forests and ultimately their value for biodiversity conservation. This „data vacuum“ (Gardner et al. 2007) invalidates any optimistic outlook on the future of biodiversity in tropical forests as proposed by Wright and Muller-Landau (2006). Better knowledge about the dynamics of faunal recovery in secondary forests is urgently needed to guide future biodiversity conservation efforts.

The loss of functional diversity in tropical secondary forests

The degree to which secondary forests can fulfill similar ecosystem functions as old-growth forest might be an even more important issue than their value for the conservation of species diversity. Biodiversity is the sum total of all biotic variation from the level of genes to ecosystems (Purvis and Hector 2000). While the concept of biodiversity is fairly simple its measurement is much more challenging. Since the concept of biodiversity is fundamentally multidimensional, no single measure will be appropriate for all dimensions. Patterns of biodiversity and its loss have most often been documented in terms of species numbers and evenness. Other facets of biodiversity are often neglected, e.g. the functional diversity of animal or plant communities. Functional diversity has been defined as “the value and range of those species and organismal traits that influence ecosystem functioning” (Tilman 2001). It is emerging as an important aspect of biodiversity as it determines the strength and shape of the relationship between species diversity and ecosystem functions (Diaz and Cabido 2001). Especially the degree to which species perform similar ecological functions in communities and ecosystems — the level of functional redundancy — is important for this relationship (Walker 1992; Lawton and Brown 1993). For example, if all species have an equal and additive effect on function (i.e. functional redundancy is low), one might expect a linear relationship between species diversity and the rate of ecosystem processes. If, on the other hand, many species are functionally redundant, the relationship between species diversity and ecosystem processes should become curvilinear. However, the relationship between species diversity and functional diversity in species-rich, natural assemblages is poorly understood (Naeem 2002). To achieve the long-term goal of restoring and managing sustainable ecosystems it is important to understand the linkages and mechanisms between species diversity and ecosystem functions, rather than species diversity as such (Walker 1992). High functional redundancy of species assemblages might indicate that ecosystem functions are robust to changes in diversity. This has important implications for the conservation of biodiversity and ecosystem functions in secondary tropical forests as it answers the question: How many species can we lose in secondary forests before we start to affect the functions of this ecosystem?

Community assembly in tropical secondary forests

Ecological dynamics in degraded systems can be very different from dynamics in less-impacted systems. For conservation of biodiversity and ecosystem functions in tropical forests, it is important to understand the feedbacks and constraints in degraded systems. We must attempt to develop better predictive tools and a broader conceptual framework to guide the restoration of degraded lands and strategies to conserve biodiversity. Little is known of the mechanisms governing the recovery of biodiversity and ecosystem processes following disturbance (Lockwood and Pimm 1999). Weiher and Keddy (1999) and Young et al. (2001) consider that assembly rules could be a useful conceptual framework for the study of the mechanisms governing the recovery of biodiversity on degraded lands. Assembly rules are generalized restrictions to coexistence, and represent constraints on how species are selected from the regional species pool to form communities (Weiher and Keddy 1999). Assembly rules inform about the factors – both biotic and abiotic – that put constraints on composition. Weiher and Keddy (1995) proposed a predictable shift in the mechanisms of community assembly along a gradient of disturbance or abiotic stress. The model predicts that under high environmental adversity, biotic factors, such as competitive interactions, will be the primary force on community composition. Conversely, under low levels of environmental adversity abiotic factors will be more important for community assembly. A successional gradient of tropical secondary forests gives opportunity to test the predictions of this model. The application of the theory of assembly rules has the potential to inform us about the factors we need to know in order to predict how communities are assembled from a common species pool. Hence, the potential utility of the theory of assembly rules in conservation and restoration ecology lies at the planning stage, to ascertain what factors might be limiting a species in a community.

One of the factors that might constrain the community assembly of ants in secondary forests are the stoichiometric balances of the habitat. As heterotrophs, ants and other invertebrates are potentially limited by access to nitrogen and phosphor (Sterner and Elser 2002). Human activities have differentially altered biogeochemical cycling at local, regional and global scales. Changes in nutrient balances in tropical secondary forests might alter the food web structure in these ecosystems. This might ulitmately also influence their value for biodiversity conservation. There is mounting interest in the field of ecological stoichiometry, defined as „the study of the balance of multiple chemical elements in ecological interactions“ (Sterner and Elser 2002). A stoichiometric approach — examining changes in nutrient balances and their effects on animal communities — may be a useful tool for a better understanding of human effects on the structure of communities and ecosystem processes.

The study area

All field work for the studies included in this dissertation was carried out in the Rio Cachoeira Nature Reserve in the Atlantic Forest of Brazil. The Atlantic Forest or *Mata Atlântica* once extended almost continuously along Brazil's Atlantic coast, from the northern state of Rio Grande do Norte south to Rio Grande do Sul (Fig. 1). It forms a narrow fringe of forest sandwiched between the ocean and the dry uplands of the planalto.

This biome has one of the highest percentages of endemism in the world. More than 8000 of an estimated 20000 species of plants are thought to be endemic. Endemism in trees is particularly high, with approximately 54% being restricted to the region (Mori et al. 1981). Likewise, many animal species are endemic to the Atlantic Forest of Brazil, e.g. 92% of the amphibians (Lynch 1979) and 948 of 2120 butterfly species (Brown et al. 2000) are found nowhere else in the world.

Figure 1: Original distribution of the Atlantic Forest in South America. Map adapted from *The Atlantic Forest Region Hotspot* map, © Conservation International.

But this biome is also one of the forests most impacted by human activities. Currently, less than 7% of the original forest cover is left (Fig. 2) and the majority of the remaining patches of old-growth forests are embedded in a mosaic of secondary forests, tree plantations, pastures, and agricultural crops (Dean 1995). This habitat loss has left large numbers of the region's endemic species severely threatened with extinction (Brooks et al. 1999). For these reasons, Brazil's coastal forests are considered as one of the five *hottest* biodiversity hotspots (Myers et al. 2000).

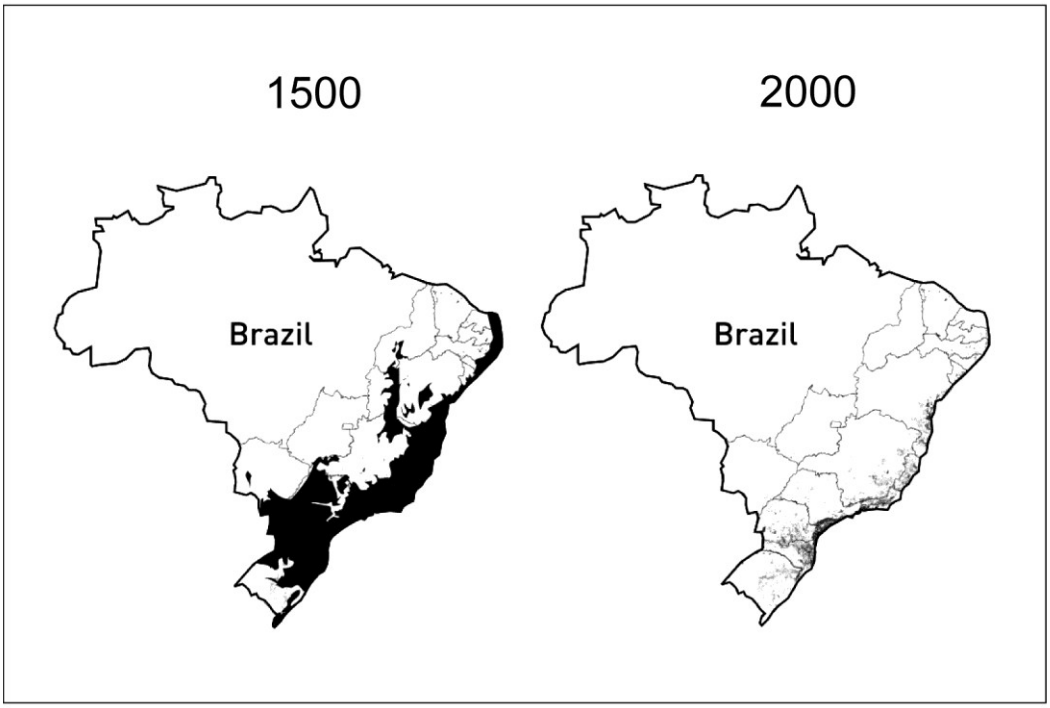

Figure 2: Original and current distribution of the Atlantic Forest in Brazil. Only ~7% of the original cover is left today.

The best-preserved areas are along the steep slopes of the coastal mountains of the Brazilian states of Rio de Janeiro, São Paulo, and Paraná. The Rio Cachoeira Nature Reserve (25°18’51”S, 48°41'45”W) is located near the city of Antonina, in the coastal region of Paraná. The 8694 ha reserve is a protected area owned and managed by the Society for Wildlife Research and Environmental Education (Sociedade de Pesquisa em Vida Selvagem e Educação Ambiental — SPVS). The regional climate is classified as Köppen’s Cfa (humid subtropical) with mean temperatures between 16.2° C in July and 24.5° C in February. Precipitation (2580 mm y^{-1}; average for 1978-1999) is well distributed throughout the year with less rain from May to August. Topography varies from littoral plains with isolated hills to the uplands of the Serra do Mar mountain range. Altitudes range from 0 to 600 m above sea level.

Lowland and submontane forests originally covered the area. But these dense ombrophilous forests suffered intense exploitation and large parts of them have been converted to pastures. Old-growth forests remain only in hillside regions. The resulting landscape mosaic consists of old-growth forests, secondary forests in various stages of succession and pastures.

Outline of this dissertation

The primary objective of this dissertation is to broaden the understanding of faunal recovery in tropical secondary forests. I used leaf-litter and soil ant communities (Hymenoptera: Formicidae) as model organisms and analyzed their recovery and related ecosystem changes during secondary forest succession in the Atlantic Forest of Brazil. The basis for the studies presented here forms the intensive sampling of ants in a total of 27 study sites in the Rio Cachoeira Nature Reserve. These study sites represent secondary forests on two different soil types and in three different regeneration phases after the abandonment of use as pastures. For each combination of soil type and successional stage, I established three replicated study sites. I collected ants from a total of 560 leaf-litter samples, 270 soil samples and 192 baiting samples. These collections resulted in ~63000 ants, which I sorted and identified (see www.ants-cachoeira.net for further information on the taxonomy, systematics and ecology of ants sampled in the course of this project). Crucial for the success of the investigations presented here was the intensive study of ant taxonomy and systematics, which lead to two additional publications: Verhaagh and Bihn (2007) and Bihn and Verhaagh (2007). The choosen sampling layout and methods allowed overcoming many of the limitations of previous studies on the recovery of ant diversity in secondary forests.

In this dissertation, I present four studies about the recovery of ant communities in secondary forests of the Atlantic Forest of Brazil, organized in chapters 2 through 5:

In **chapter 2**, I report on the recovery of ant communities in tropical secondary forests using "classical" measures of biodiversity — the richness of taxa and the composition of communities. For this purpose, I established 27 sites that encompassed a chronosequence from pastures to old-growth forests on two contrasting soil types. The results are based on a collection of 35508 ants in 40 genera. I describe the effects of secondary succession on the structure of epigeic and hypogeic ant communities and analyze the influence of soil type on the recovery process. Furthermore, estimates for the time that is necessary for the complete recovery of ant diversity in secondary forests are provided.

Chapter 3 is concerned with the changes in functional diversity of ant communities during tropical forest succession. Biodiversity has a multitude of facets that can be quantified but has most often be measured as species richness – the number of species at a locality. Measures of functional diversity include the functional differences among species. The functional diversity of communities, rather than species diversity, may be crucial for ecosystem functioning. My analysis uses a continuous measure of functional diversity and is based on four functional traits related to resource use of ants: body size, relative eye size, relative leg length and trophic position.

Chapter 4 deals with the community assembly of leaf-litter ants in tropical secondary forests. A better understanding of the mechanism that lead to the assembly of local communities from the regional species pool is necessary to predict the consequences of anthropogenic disturbances on biodiversity. This analysis is based on the distribution of coexisting ant species in niche space, the axes of which are defined by the functional traits of species (body size and trophic position). Ants were sampled from 240 one-square-meter quadrats. In order to identify the prevalent mechanism of community assembly, I tested for non-random patterns in niche space occupation of these 240 assemblages, comparing observed patterns with expected patterns based on two null models. The niche space was characterized by estimating the total space occupied and the mean nearest neighbor distances between species. Additionally, I analyzed if significant changes in the pattern of niche space occupation occur along a successional gradient of forests.

In **chapter 5**, I investigate changes in ecological stoichiometry during tropical forest succession based on the food preferences of ants. From a human perspective, the degree to which secondary forests can provide ecological services might be more important than their value for biodiversity conservation. The balance of energy and multiple chemical elements in ecological interactions (ecological stoichiometry) has important consequences for the ecological functions and services of ecosystems. I analyzed leaf-litter ants from different successional stages of secondary forests in their preference for baits that contained carbohydrate or protein resources and compared their preferences to those from old-growth forests. The study is based on the premise that ant workers prefer the scarcer resource when confronted with alternatives. If there are differences in the stoichiometric balances provided by secondary and old-growth forests, one would expect a shift in the ants‘ preference for one of the two different bait types.

Chapters 2-5 of this dissertation have been published, are submitted or are in preparation for submission to journals. They are closed entities that can be read independently of each other. This structure, however, leads to some redundancy in content among the chapters.

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2 Do secondary forests act as refuges for old-growth forest animals?

Recovery of ant diversity in the Atlantic Forest of Brazil

with Manfred Verhaagh, Martin Brändle and Roland Brandl

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Abstract

The extent to which secondary forests occupying degraded and abandoned lands provide suitable habitat for forest-adapted species is an important conservation issue in times of vanishing old-growth forests. We used ants (Hymenoptera: Formicidae), a functionally important and diverse group of invertebrates, to investigate the recovery of soil taxa during secondary forest succession in the Atlantic Forest of Southern Brazil. We compared the resilience of epigeic versus hypogeic ant assemblages. For this purpose we established 27 sites that encompassed a chronosequence from pastures to old-growth forests on two contrasting soil types. Our results are based on a collection of 35 508 individuals in 40 genera.

Richness and composition of ant assemblages in secondary forests have recovered slowly and have not approached conditions typical of old-growth forests. The distribution of genera along the successional stages was arranged in a nested pattern where ant genera of younger successional stages were a subset of genera present in older stages. Edaphic conditions had no influence on the recovery process. Overall, richness of ants was lower at study sites with water-logged soils than at sites where soils did not exhibit hydromorphic properties. The hypogeic ant assemblage recovered more slowly than the epigeic assemblage.

Our results show that secondary forests do not act as refuges for many forest-adapted animals which are currently restricted to discontinuous patches of old-growth forest in the highly endangered Atlantic Forest of Brazil. Moreover, estimated recovery times of 50 to several hundred years suggest it would take much longer than previously presumed for complete recolonization.

Introduction

The loss of tropical forests has been identified as a major pressure on global biodiversity (Jenkins 1992; Whitmore and Sayer 1992; Pimm and Raven 2000). Some researchers have proposed extinctions rates comparable with the five mass-extinctions during the phanerozoicum (May et al. 1995). Recently, however, Wright and Muller-Landau (2006) questioned that tropical biodiversity is at the verge of extinction. Their analysis showed that the remaining forest cover depends on human population density in rural areas. Since rural populations are supposed to decrease in the near future, net forest loss might be lower than previously expected, which should lead to decreasing extinction rates (Wright and Muller-Landau 2006). This provocative paper generated a vigorous debate about the tropical biodiversity crisis (e.g. Laurance 2007; Gardner et al. 2007). One of the key assumptions used by Wright and Muller-Landau is that secondary forests serve as refugia for old-growth forest species (Laurance 2007). The potential of secondary forests for conservation of old-growth forest species is, however, an area of much uncertainty. Hence, quantification of the value of secondary forests as habitat for forest-adapted plant or animal communities is a crucial factor in the prediction of future biodiversity in the tropics. Although the negative consequences of clear-cutting and forest to farmland conversion on forest biodiversity are well documented (e.g. Holloway 1987; Verhaagh 1991; Eggleton et al. 1995), little is known about the dynamics of biodiversity during tropical forest succession.

Soils harbor the most species-rich communities of terrestrial ecosystems (Giller 1996). Besides their extraordinary diversity, soil animals are important triggers of ecosystem processes (Wardle 2002; Mikola et al. 2002; Lavelle et al. 2006). However, the processes that influence distribution and abundance of soil communities remain poorly understood (Giller 1996; Bardgett 2002). For instance, our knowledge about the impact of disturbances on belowground communities is very limited (Giller et al. 1997; Bengtsson 2002; Mathieu et al. 2005). To evaluate the effects of disturbance on a community, it is necessary to distinguish between resistance and resilience. While resistance describes the degree to which a system is altered when the environment changes, resilience is the rate at which a system returns to its original state (sensu Pimm 1984). Bengtsson (2002) proposed that soil communities exhibit a low resilience.

Vertical stratification appears to be a pronounced feature of ant distributions in tropical forests with each stratum (e.g. subterranean, leaf-litter, canopy) sustaining distinct communities (Vasconcelos and Vilhena 2006; Ryder Wilkie et al.

2007). In comparison to the subterranean stratum, the leaf-litter stratum is a rather ephemeral habitat and more exposed to climatic extremes in temperature and humidity. Leaf-litter ants are often generalists, e.g. for nesting sites (Byrne 1994) and food (Delabie and Fowler 1995). Many ants in the leaf-litter are constantly moving between nesting sites which might favor the rapid recolonization of disturbed sites (McGlynn et al. 1994). These differences in the ecological characteristics of ants associated with leaf-litter or subterranean habitats may lead to divergence in the resilience of the respective communities.

Ants (Hymenoptera: Formicidae) are a dominant invertebrate group in tropical forests. The strong interactions between ants and other organisms make the former important "keystone species" in tropical forests. Furthermore, ants structure their environment through their roles as seed dispersers (Beattie 1985; Levey and Byrne 1993), predators (Andersen 1992; Kaspari 1996a; Philpott and Armbrecht 2006) and ecosystem engineers (Lobry de Bruyn and Conacher 1990; Folgarait 1998). Ants are therefore "driver" species in the context of Walker's "driver and passengers" hypothesis, and abundance, as well as diversity, of ants should trigger ecosystem functions (Walker 1995). Given their importance, ants are an obvious choice for biodiversity studies.

We examined the diversity of leaf-litter (epigeic) and soil (hypogeic) ant assemblages along a successional gradient from pastures, through three age stages of secondary forest to old-growth forests in the Atlantic Forest in Southern Brazil. The Brazilian Atlantic Forest is considered one of the "hottest hotspots" of biodiversity. Unfortunately, this biome is also experiencing an exceptional degree of habitat loss (Myers et al. 2000). During the last 500 years, more than 90% of the Atlantic Forest has disappeared and most remaining forests are secondary, rather than old-growth (Dean 1995). In this study, we examined whether secondary forests of the Brazilian Atlantic Forest act as refugia for forest adapted species using epigeic and hypogeic assemblages of ants as a model. Specifically, we addressed the following questions:

(1) Are species richness and species composition of ant assemblages across a gradient of tropical forest succession related to successional stages?

(2) Do edaphic conditions alter the recovery of ant assemblages?

(3) Do hypogeic ant assemblages exhibit a lower resilience (i.e., speed of return to the reference state) than epigeic assemblages?

Methods

Research area

The Rio Cachoeira Nature Reserve (25°18’51”S, 48°41'45”W) is located near the city of Antonina, in the coastal region of the Brazilian state of Paraná. The ~12 000 ha reserve is a protected area owned and managed by the Sociedade de Pesquisa em Vida Selvagem e Educação Ambiental (SPVS). The regional climate is classified as Köppen’s Cfa (humid subtropical) with mean temperatures between 16.2° C in July and 24.5° C in February. Precipitation (2580 mm y^{-1}; averages for 1978-1999) is well distributed throughout the year with less rain from May to August. Topography varies from littoral plains with isolated hills to the uplands of the Serra do Mar mountain range. Altitudes range from 0 to 600 m above sea level.

Lowland and submontane forests originally covered the area. But these dense ombrophilous forests suffered intense exploitation and large parts of them have been converted to pastures. Old-growth forests remain only in hillside regions. The resulting landscape mosaic consists of old-growth forests and secondary forests in various stages of succession and pastures.

Study Sites

Between June and September 2003 we sampled the ant fauna in 27 sites scattered across the reserve (Fig. 1). The lowest sites are at 10 m above sea level and the highest site is located at 260 m above sea level. We sampled ants along a chronosequence and from two soil types according to a two-way factorial design with three replicated sites for each combination of the two factors. The first factor focused on the time scale of succession after abandonment of buffalo ranching. The forest succession age stages were very young secondary forest (~5 years; stage 1), young secondary forest (10-15 years; stage 2), and old secondary forest (35-50 years; stage 3). Land-use history for study sites were established through interviews with residents and reserve staff and corroborated by inspection of high resolution, geocoded orthophotos from the years 1952, 1980 and 2002 in a GIS environment. The two contrasting soil types were Gleysols and Cambisols which differ in soil drainage. During part of the year, ground water in Gleysols rises to a point 50 cm or less below the surface, whereas Cambisols do not show hydromorphic properties. We sampled ants in three old-growth forests (sensu Clark 1996; stage 4) on Cambisols as a reference stage. Stage 4 on Gleysols could not be found in the reserve. We also sampled pastures (stage 0) on both soil types in order to obtain information on ant assemblages in the agricultural matrix.

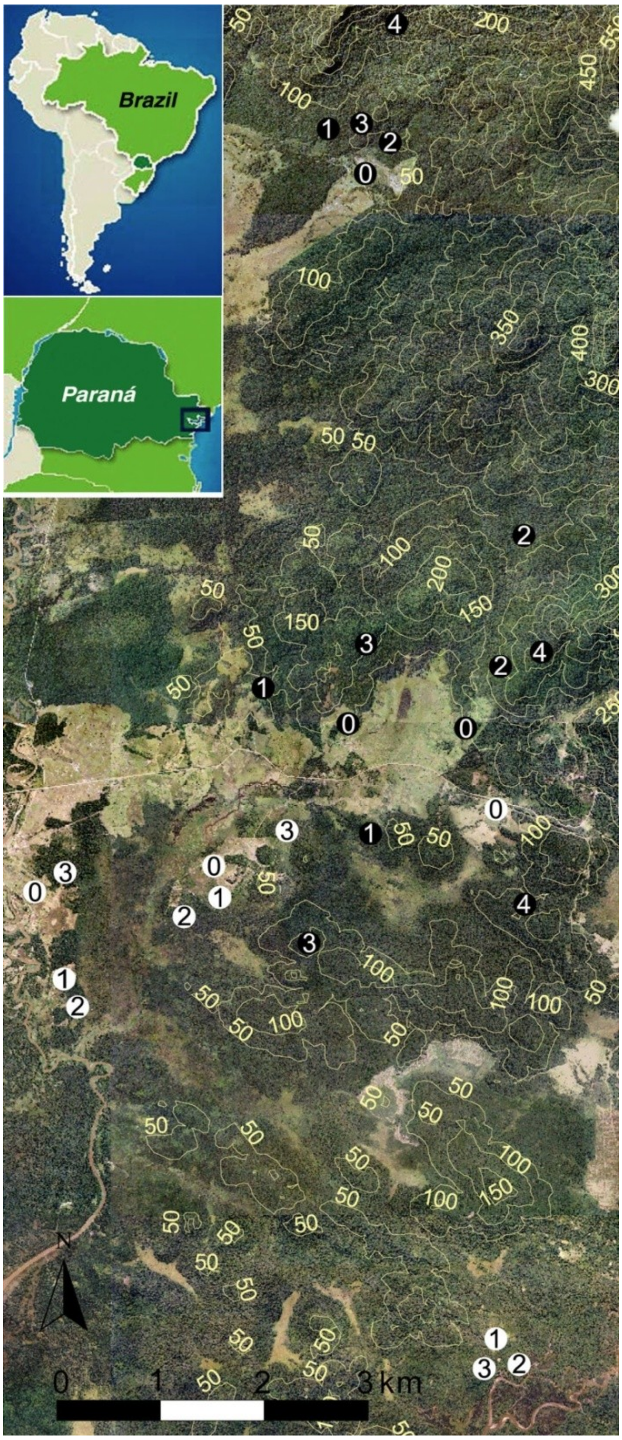

Figure 1. Location of study sites at Rio Cachoeira Nature Reserve with altitudinal isolines. Numbers in- dicate successional stages 0 to 4 (white circles: sites on Gleysol; black circles: sites on Cambisol).

Sampling methods

At each study site we established two, 50 m transects (parallel, separated by 20 m) and collected samples at 10 m intervals along these transects (five sampling points for each transect). At each sampling point we collected one litter sample and one soil sample in 1 m distance to the transect on opposing sides. This resulted in 10 litter samples and 10 soil samples for each study site. Transects were located at least 50 m from any trail, pasture or any other habitat in order to minimize edge effects (Didham 1997).

For sampling of epigeic ants (litter samples), we collected all leaf litter and twigs inside a quadrate of 1 m^2 and sifted all litter material through a 1 cm mesh screen. Ants were extracted by leaving the sifted material in Winkler bags for 3 days (see Agosti et al. 2000 for a detailed description of the method). We took samples of hypogeic ants (soil samples) by excavating cubes of 15 cm x 15 cm x 10 cm from the upper soil layer (without leaf litter), followed by extraction of the fauna using Berlese funnels for 21 days. Worker ants were sorted to genera following the nomenclature of Bolton (2003). Voucher specimens were deposited at the Museu de Zoologia da Universidade de São Paulo (MZUSP).

Statistical Analysis

To explore patterns of ant diversity, we used genera as a surrogate to estimate species richness and composition of the ant assemblage. It has been demonstrated on global, continental (Gaston and Williams 1993; Williams and Gaston 1994) and local scales (Andersen 1995; Balmford et al. 1996) that higher-taxon richness reflects patterns of species richness.

Because ants are social insects, distribution of individuals within samples is clumped. A single sample may contain high numbers of individuals of a rare genus (Longino 2000). To minimize the problem of clumping we used, as a measure for abundance, the presence of genera across the samples of a site (the frequency of occurrence). Therefore, the theoretical maximum of a species "abundance" at a specific site is 10. The observed number of taxa in a community is a biased estimate of real community richness (Colwell and Coddington 1994). We estimated the expected total number of genera for each site using the Chao2 estimator (EstimateS version 7.5; Colwell 2005) in order to compare completeness of our sampling between different habitats and sampling methods. Differences in taxon richness can arise because of differences in sample size among collections. Therefore, we adjusted genera richness per site to the lowest common number of occurrences using rarefaction as implemented in EcoSim (version 7.72; Gotelli and Entsminger 2005).

We analyzed our estimates of ant genera richness using a repeated measures ANOVA to test for the effects of successional stage (stages 1-4), soil type (Gleysols vs. Cambisols) and their interactions in a sequential order (type I sum of squares). By including soil type as the first factor in the model, we avoided misinterpretations of tests for the subsequent factors (and interactions) in the model due to the missing old-growth forest sites on Gleysol. The habitat (epigeic vs. hypogeic) of ant assemblages at each site comprised the repeated measure. The response variables were (i) the observed number of genera, (ii) the rarefied number of genera and (iii) genera density per site (mean number of genera occurrences in 10 samples).

Permutational multivariate analysis of variance (PERMANOVA version 1.6; Anderson 2001) was used to analyze the changes in genera composition of ant assemblages among successional stages (stages 1-3) and among soil types (Cambisol vs. Gleysol). This was done in two separate analyses for epigeic ants and for hypogeic ants. Additionally, we tested the effect of successional stages on the composition of genera including only sites on Cambisol (stages 1-4). We tested the main factors and their interaction terms with 999 permutations of residuals under the full model, using Chi^2 distances among sites.

When composition of genera-poor sites represents a subset of genera-rich sites, the pattern is called nestedness or nested subsets (Atmar and Patterson 1993). We explored nestedness according to Leibold and Mikkelson (2002). A correlation between genera richness and site scores of a correspondence analysis implies nestedness. To further visualize nestedness of genera distribution across the successional stages, we used statistical seriation, an unidimensional method that seeks the best enumeration order of a set of objects (PermutMatrix version 1.7.c; Caraux and Pinloche 2005). Seriation was calculated with the unidimensional scaling algorithm and discrete optimization. The order of successional stages (columns) was fixed whereas seriation arranged the order of genera for the optimal linear arrangement. By using genera to calculate nestedness we assume that all species of a genus have similar ecological niches and thus show similar distributions along the successional gradient. However, significant patterns of nestedness on the level of genera are conservative estimates for the nestedness on the species level: genera composed of species with widely different niches will decrease nestedness on the genus level.

Results

Across the 27 sample sites we found 35 508 worker ants: 23 821 from epigeic samples and 11 687 from hypogeic samples. We recorded 40 ant genera, with 13 being specific to epigeic samples, but only one genus specific to the hypogeic samples. Chao2 estimates indicated a high level of sample completeness with observed richness ranging between 64% and 98% of estimated richness (Table 1). A list of all ants sampled is available at http://www.ants-cachoeira.net or from the first author.

Richness of genera

Genera richness per site ranged from 9 to 22 (mean = 14.8, SE ± 0.8) for litter ants and varied with successional stage and soil type (Table 1). With 3 to 14 genera (mean = 7.9, SE ± 0.6) per site, richness was much lower for hypogeic ants than for epigeic ants (Table 1). Genera richness in pastures was much lower than in forest habitats. Observed and rarefied genera richness increased with successional stage (Table 2, Fig. 2). Richness was generally lower in Gleysol sites than in Cambisol sites, but the increase in number and density of genera for both soil types followed a similar general pattern. Nevertheless, we found significant interacting effects of successional stage and habitat on the richness and density of genera (Table 2): Richness of epigeic ant genera increased faster than the richness of genera from soil samples (Fig. 2).

Table 1. Abundance and diversity of ants along successional stages in the Atlantic Forest. Means (±SE) of sites for each combination of successional stage, soil type and habitat.

Soil type	Cambisol					Gleysol			
Succession stage[a]	0	1	2	3	4	0	1	2	3
Epigeic ants									
Number of genera	10	11.3 ± 1.2	15.3 ± 0.3	17.7 ± 1.8	21.7 ± 0.3	9	11.7 ± 0.9	13.7 ± 0.9	15.7 ± 2.0
Total number of genera[b]		19	20	27	30		16	21	23
Chao2[c]	11	15 ± 3.8	18 ± 1.5	19 ± 1.8	23 ± 0.5	12	13 ± 0.6	18 ± 2.7	19 ± 2.4
Completeness (%)[d]	94	80	88	95	93	77	93	78	82
Rarefaction[e]		9.9 ± 0.8	11.7 ± 0.3	12.9 ± 1.0	14.5 ± 0.2		10.5 ± 0.3	11.1 ± 0.3	12.2 ± 0.9
Abundance	163	471 ± 112	1278 ± 308	1428 ± 273	2703 ± 289	243	211 ± 72	876 ± 421	832 ± 248
Genera occurrences	30	50 ± 2	69 ± 5	82 ± 8	92 ± 2	31	41 ± 7	57 ± 9	59 ± 9
Hypogeic ants									
Number of genera	3.7 ± 0.7	8.3 ± 0.9	8.3 ± 0.9	9.3 ± 0.9	12.0 ± 1.0	4.0 ± 0.6	7.3 ± 1.2	7.7 ± 1.9	10.3 ± 0.3
Total number of genera[b]	7	12	11	16	17	7	11	12	16
Chao2[c]	4 ± 0.9	9 ± 0.9	10 ± 1.6	14 ± 0.2	16 ± 2.0	5 ± 1.1	9± 1.7	8 ± 2.1	16 ± 1.0
Completeness (%)[d]	87	98	88	68	78	82	86	92	64
Rarefaction[e]		5.0 ± 0.2	4.9 ± 0.3	5.4 ± 0.3	6.0 ± 0.1		4.5 ± 0.3	4.8 ± 0.4	5.5 ± 0.2
Abundance	385 ± 215	634 ± 351	503 ± 88	180 ± 37	201 ± 99	479 ± 453	766 ± 486	411 ± 204	336 ± 104
Genera occurrences	14 ± 3	32 ± 5	32 ± 1	24 ± 1	29 ± 4	10 ± 1	24 ± 5	26 ± 9	25 ± 3

[a] Numbers indicate stages of forest succession: 0: pasture; 1: ~5 years after abandonment; 2: 10-15 years after abandonment; 3: 35-50 years after abandonment; 4: old-growth forest. For each combination of soil type and regeneration stage n = 3, except for epigeic ants in pastures where n = 1.

[b] Pooled number of genera for each combination of successional stage, soil type and habitat.

[c] Estimates of true genera richness from Chao2 richness estimator with 100 randomizations without replacement.

[d] Percentage of Chao2 estimate compared to observed number of genera.

[e] Rarefaction to a common number of occurrences. For epigeic ants the number of genera is standardized to 29 occurrences and for hypogeic ants to 8 occurrences.

Table 2. Results of repeated-measures ANOVAs on the effects of soil type, successional stage, and habitat (and their interactions) on the observed number of genera, rarefied number of genera and genera density.

	Source of variation	SS (type I)	df	MS	F	p
Genera per site	*Between subjects*					
	Soil type[a]	38.89	1	38.89	7.42	0.016
	Successional stage[b]	194.94	3	64.98	12.41	< 0.001
	Soil type[a] x successional stage[b]	1.17	2	0.58	0.11	0.895
	Error	73.33	14	5.24		
	Within subjects					
	Habitat[c]	408.59	1	408.59	145.43	< 0.001
	Habitat[c] x soil type[a]	8.13	1	8.13	2.89	0.111
	Habitat[c] x successional stage[b]	32.39	3	10.79	3.84	0.034
	Habitat[c] x succession[b] x soil[a]	7.06	2	3.53	1.26	0.315
	Error	39.33	14	2.81		
Rarefied genera[d]	*Between subjects*					
	Soil type[a]	4.79	1	4.79	6.39	0.024
	Successional stage[b]	29.87	3	9.96	13.29	< 0.001
	Soil type[a] x successional stage[b]	0.31	2	0.16	0.21	0.816
	Error	10.49	14	0.75		
	Within subjects					
	Habitat[c]	468.38	1	468.38	665.06	< 0.001
	Habitat[c] x soil type[a]	0.83	1	0.83	1.18	0.296
	Habitat[c] x successional stage[b]	8.94	3	2.98	4.23	0.025
	Habitat[c] x succession[b] x soil[a]	1.56	2	0.78	1.11	0.358
	Error	9.86	14	0.70		
Genera density	*Between subjects*					
	Soil type[a]	16.39	1	16.39	9.81	0.007
	Successional stage[b]	15.01	3	5.01	2.99	0.067
	Soil type[a] x successional stage[b]	0.11	2	0.06	0.03	0.968
	Error	23.39	14	1.67		
	Within subjects					
	Habitat[c]	144.49	1	144.49	413.66	< 0.001
	Habitat[c] x soil type[a]	7.50	1	7.50	21.49	< 0.001
	Habitat[c] x successional stage[b]	21.06	3	7.02	20.09	< 0.001
	Habitat[c] x succession[b] x soil[a]	2.17	2	1.09	3.11	0.076
	Error	4.89	14	0.35		

[a] levels: Cambisol, Gleysol.

[b] levels: ~5 years after abandonment, 10-15 years after abandonment, 35-50 years after abandonment, old-growth forest (> 100 years).

[c] levels: soil, leaf litter.

[d] number of genera per site after rarefaction to a common number of occurrences among all sites for each habitat (29 occurrences for ants from the leaf litter; 8 occurrences for ants from soil samples).

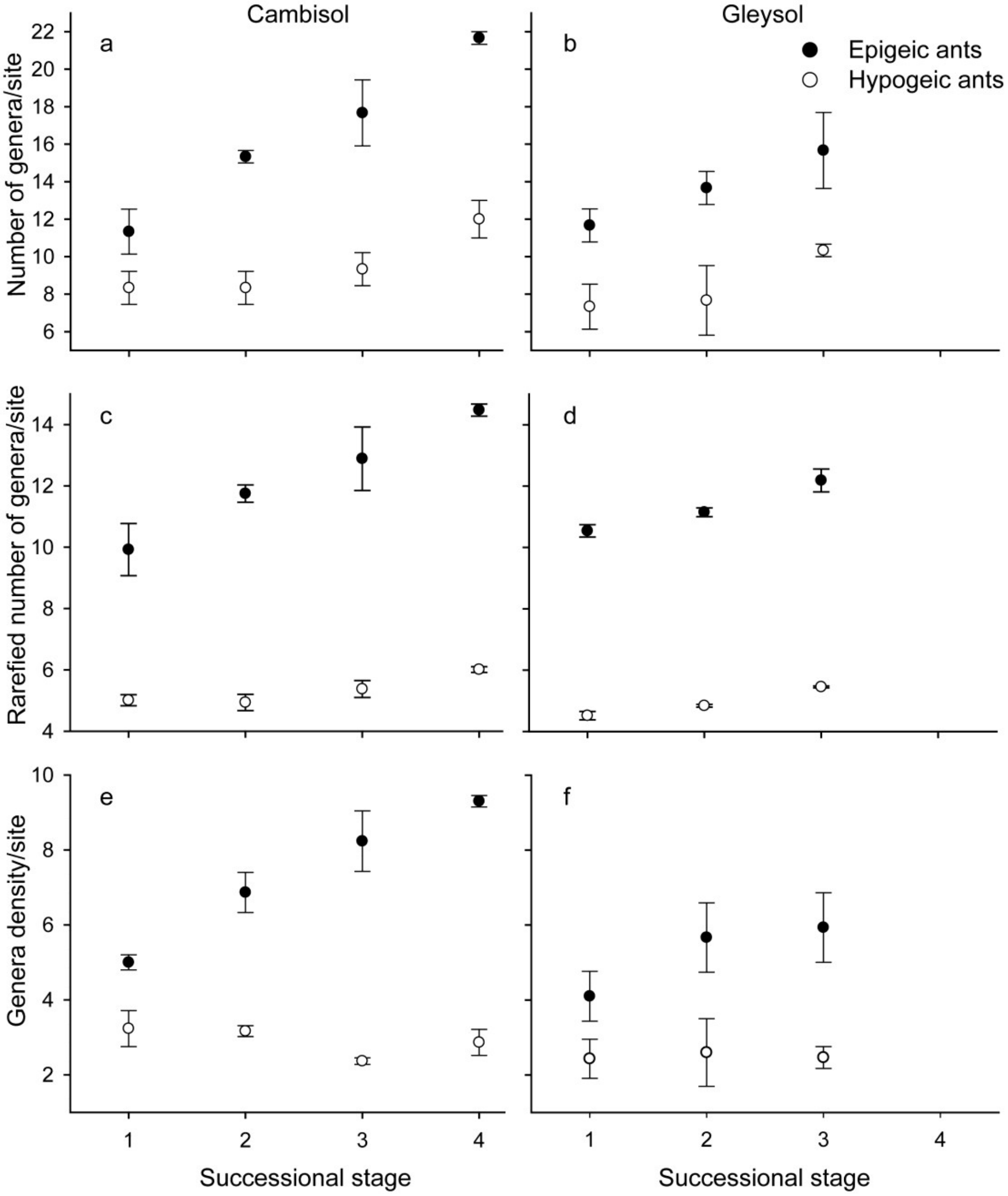

Figure 2. Mean richness of genera (± SE) per study site (n = 3; a & b), mean richness of genera per study site after rarefaction (± SE) to a common number of occurrences (c & d) and mean (± SE) of density of genera per study site (mean number of genera occurrences in 10 samples per site; e & f) for epigeic and hypogeic ants at different stages of forest succession.

Composition of assemblages

Composition of the epigeic ant assemblages differed among successional stages (Cambisol & Gleysol sites, stages 1-3: $p = 0.04$; only Cambisol sites, stages 1-4: p

< 0.01). Soil type did have an effect on the epigeic ant assemblage (p = 0.03) but the change in genera composition among successional stages was not influenced by soil type (p = 0.38). The change in assemblage composition of the hypogeic assemblages among successional stages 1-3 (secondary forests) was not significant (p = 0.56). If we considered only sites on Cambisol and included stage 4 (old-growth forest) in the analysis, succession did have a significant effect on composition (p = 0.02). Soil type had no significant effect on hypogeic genera composition (p = 0.12) nor did it modulate the change in genera composition associated with successional stages (p = 0.11). This combination of results suggests that the regeneration of the ant communities along the successional gradient differed between the epigeic and hypogeic assemblage.

Based on the seriation (Fig. 3a-3d), the epigeic fauna showed a strong tendency towards nestedness, while the hypogeic fauna did not. This was also supported by correlation of the number of genera with the first axis of a correspondence analysis. Genera richness was strongly correlated with sample scores of the epigeic samples (sites on Cambisols: R = -0.82; sites on Gleysols: R = -0.75) but not with scores of the hypogeic fauna (sites on Cambisols: R = 0.53; sites on Gleysols: R = -0.19).

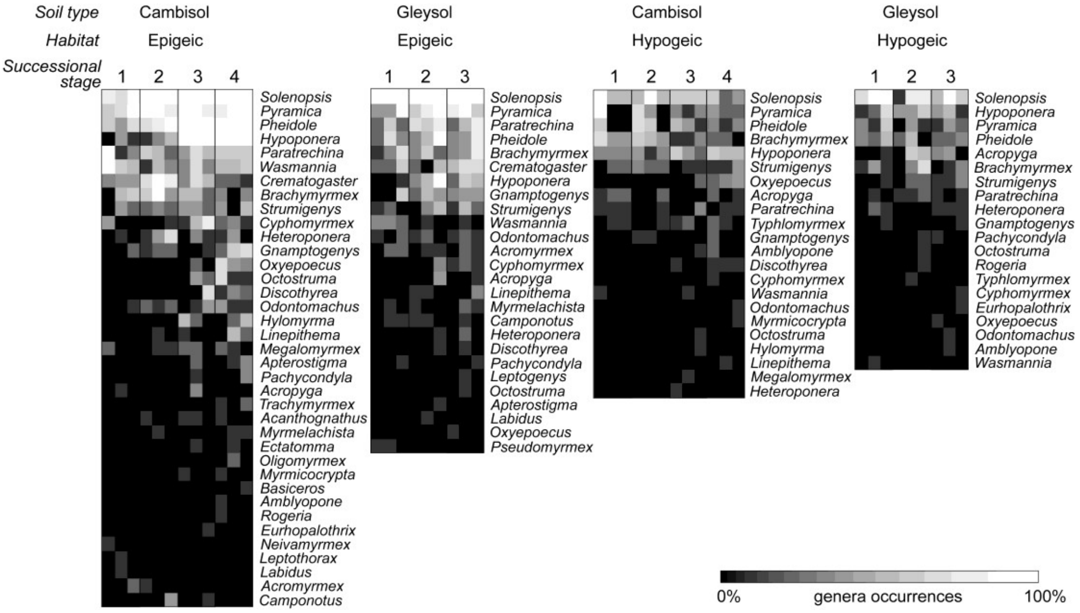

Figure 3. Seriation analysis of the distribution of genera across the successional stages. Cell shading corresponds to the frequency of occurrences in 10 samples per site, with lighter shading corresponding to higher occurrences. Columns represent study sites (three replicated sites for each successional stage) ordered in a fixed sequence of increasing successional stage.

Discussion

Recovery of the ant assemblage

The conversion of old-growth forests into pastures led to a drastic decrease of richness in ant genera, which is consistent with other studies (e.g. Verhaagh 1991; Roth et al. 1994; Vasconcelos 1999). Once pastures are abandoned, forest regeneration begins and diversity as well as composition of the original ant communities recovered gradually. However, in contrast to conclusions reached in other studies (e.g., Belshaw and Bolton 1993; Lawton et al. 1998; Vasconcelos 1999; Kalif et al. 2001), even 35 to 50 year old secondary forests had significantly lower ant richness (LSD post hoc test for observed and rarefied richness: $p < 0.02$) and composition of ant assemblages in these successional forests differed from old-growth forests. This difference between our findings and published studies may be due to differences in land use history. Secondary forests in the studies of Kalif et al. (2001), Lawton et al. (1998) and Watt et al. (2002) were never used as pastures and/or were only selectively logged. The ant communities in secondary forests which were established on former pastures seem to recover more slowly than in areas where the land is less drastically disturbed when succession begins. Nestedness was a prominent feature of the epigeic ant assemblages. 16 out of 40 genera showed a significant increase in occurrence with increasing successional age (results of correlation analyses between occurrence of individual genera and site scores on first CA-axis). Moreover, five out of 39 leaf-litter dwelling genera (*Amblyopone*, *Basiceros*, *Oligomyrmex*, *Rogeria* and *Trachymyrmex*) were restricted to old-growth forests. This pattern suggests that critical resources on which genera rely are distributed in a similar nested way and, therefore, at least some resources are restricted to old-growth forest. From these data it seems apparent that even a combination of various (successional stages of) secondary forests does not sustain biodiversity levels that are typical of old-growth forests.

In a meta-analysis on the recovery of animal communities during tropical forest regeneration, Dunn (2004) estimates that recovery of ant species richness is completed after 20 to 40 years. A similar analysis of our data, however, indicated a time frame for recovery of 50 to several hundred years (Fig. 4). We believe that, for at least two reasons, this is a conservative estimate. First, it has been shown that some hyperdiverse ant genera (e.g., *Pheidole, Camponotus*) are more species-rich in old-growth, than in disturbed, forests (Kalif et al. 2001). Hence the differences in species richness between secondary forests and old-growth forests should be more pronounced on the species level than on the genus level. Second, our estimates were derived from a simple linear regression. Communities, however, will approach the status of old-growth forests in a nonlinear, asymptotic way which also increases the time frame of recovery (Simberloff and Wilson 1970). Although our interpretations are compromised by large confidence intervals (Fig. 4), our analysis shows that, if all things go wrong, regeneration of forest communities may need 100 years and more. Decisions for the conservation of biodiversity should be based on such *worst case scenarios*!

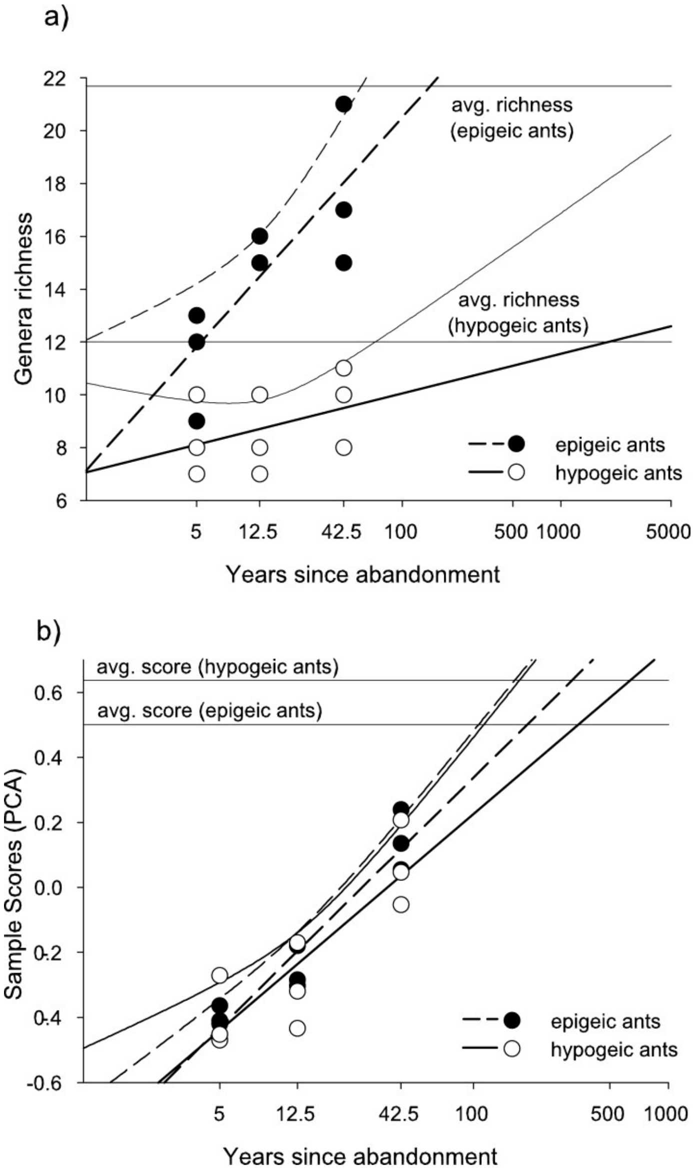

Figure 4. Genera richness (a) and genera composition (b) vs. $\log_{10}$ (years since abandonment) by habitat for sites on Cambisol. Each point represents the number of genera (a) or sample scores on the first axis of a principle component analysis after coordinate rotation (b) of the hypogeic or epigeic ant assemblage at a site during forest succession. Regression lines (and 95% lower confidence intervals) and average values of assemblages in old-growth forests for epigeic and hypogeic ants are shown.

Influence of soil type on ant assemblage recovery

We found no evidence that the recovery of ant diversity depends on the physical conditions of soils. The overall number of ant genera was lower on Gleysols and ant assemblage composition differed between soil types (i.e. for epigeic ants). The harsh physical conditions in Gleysols (water-saturated substrate) may act as a strong filter, restricting the pool of potential colonists. Investigations on the effect of soil type on the ant fauna are scarce, but Way et al. (1997) demonstrates that "certain soils prevent the spread of *Linepithema humile* in agricultural systems." Johnson (1992) reports that soil texture influences the distribution of two desert ant species. In a study of the effects of topography on the distribution of ground-dwelling ants in central Amazonia, Vasconcelos (2003) finds that the structure of the local ant fauna differs according to soil conditions. Our results suggest that the recovery pattern of the ant assemblages does not depend on physical soil properties but the composition of local ant assemblages might depend on edaphic conditions.

Resilience of the epigeic vs. hypogeic ant assemblage

The recovery of genera richness, as well as genera composition, of the epigeic ant community proceeded slowly toward conditions reflective of those in old-growth forests. The hypogeic assemblage, however, did not demonstrate a gradual recovery toward ant assemblage characteristics found in old-growth forests. For the time frame under study our results indicate a lower resilience of the hypogeic in comparison to the epigeic ant assemblage. Initially, after abandonment of pastures, ants rapidly recolonized hypogeic habitats but in subsequent successional stages of secondary forests the number of hypogeic ant genera was almost constant among stages but always lower than in old-growth forests. A similar pattern was found for the composition of the hypogeic assemblage. Different successional stages of secondary forests had no effect on genera composition but the composition changed significantly in old-growth forests. In addition, the lack of a nested pattern in genera distribution of hypogeic assemblages was striking (Fig. 4) and point to high turnover of genera among successional stages. Different conclusions can be drawn from this result: (i) hypogeic assemblages remained substantially disturbed in secondary forests and little resembled the assemblages of old-growth forests, or (ii) recovery of ant assemblages followed different pathways, i.e. recovery rates differed during the recovery process between the two soil habitats. An analysis on species level should be able to discriminate better between these alternatives.

Resources (e.g. nest sites and food) on which ants depend (Culver 1974; Kaspari 1996b), might recover more slowly under the soil surface than in the leaf litter. Once a closed canopy cover is developed, litter fall creates a leaf litter habitat that is similar in its structure to old-growth forests. Below surface habitats may be only loosely correlated to aboveground succession (De Deyn and Van der Putten 2005). The diversity of microhabitats and associated fauna require a longer period of time to recover and gain the chemical, physical and biological states that are characteristic of old-growth forests.

The lower resilience of the hypogeic ant assemblage in comparison to the leaf-litter assemblage may also be rooted in their ecological characteristics. Delabie and Fowler (1995) argue that many hypogeic ants are dietary specialists. Specialized animals might need more time to recolonize a habitat that was severely disturbed by its use as pasture. Ants which build deep and secure nests in the soil often remain at the same site for many years. Ant colonies in the leaf-litter move their nests frequently with residence time of only several weeks (Byrne 1994). This high mobility of leaf-litter ants may contribute to the observed faster recolonization of disturbed sites in comparison to subterranean ants.

Implications for conservation

There is still considerable disagreement regarding the ongoing loss of tropical forests and the estimated consequences for forest biodiversity (Laurance 2007). The debate about future predictions of extinctions bears a high level of uncertainty because (i) it is unclear if, and to what extend, secondary and degraded habitats can serve as refugia for forest species and (ii) most species of small-bodied taxa, which account for the vast majority of species in tropical forest, are undescribed; their distribution in, and dependence on, old-growth forests are unknown.

Our results, based on small-bodied animals, show that a mere aggregation of trees (e.g., secondary forests, degraded forests and plantations) does not constitute a *forest* for forest species. A considerable fraction of the ant community depends on old-growth forest. Therefore the value for biodiversity conservation of secondary forests is not comparable to old-growth forests because they only sustain a depauperate subset of species. Furthermore, regeneration of ant diversity in secondary forests is slow. Even 35 to 50 year old secondary forests had a lower genera richness and altered composition in comparison to old-growth forests. Our speculative but conservative estimates indicate that complete recovery of the ant community may require several hundred years. The obvious importance of old-growth forests for preservation of forest biodiversity is even more pronounced in biodiversity hotspots with high levels of endemism.

Different taxa recover at different rates during forest regeneration and no taxon has proved to be a particularly good predictor of the richness of other taxa (Wolters et al. 2006). Furthermore, our results show that even *within* a single taxon different assemblages that inhabit the same forest, but different strata within, may react quite differently to anthropogenic disturbance. The assessment of the value of tropical secondary forests through evaluation of the diversity of a single taxon might, therefore, not only result in a misleading picture of overall biodiversity, but also an erroneous indication of the diversity of other assemblages within the studied taxon. We feel that inclusion of different assemblages of several taxa is the most appropriate approach in models designed to evaluate secondary forest as a habitat for forest-adapted species.

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3

Loss of functional diversity of ant assemblages in secondary tropical forests

with Gerhard Gebauer and Roland Brandl
submitted

Abstract

Secondary forests and plantations increasingly dominate the tropical wooded landscape in place of primary forests. The expected reduction of biodiversity and its impact on ecological functions provided by these secondary forests are of major concern to society and ecologists. The potential effect of biodiversity loss on ecosystem functioning depends largely on the associated loss in the functional diversity of animal and plant assemblages, i.e. the degree of functional redundancy among species. However, the relationship between species and functional diversity is still poorly documented for most ecosystems. Here, we analyze how changes in the species diversity of ground foraging ant assemblages translate into changes of functional diversity along a successional gradient of secondary forests in the Atlantic Forest of Brazil. Our analysis uses a continuous measure of functional diversity and is based on four functional traits related to resource use of ants: body size, relative eye size, relative leg length and trophic position. We find a strong relationship between species and functional diversity, independent of the functional traits used, with no evidence for saturation in this relationship. Recovery of species richness and diversity of ant assemblages in tropical secondary forests were accompanied by a proportional increase of functional richness and diversity of assemblages. Moreover, our results indicate that the increase in functional diversity along the successional gradient of secondary forests is primarily driven by rare species, which are functionally unique. The observed loss of both species and functional diversity in secondary forests offers no reason to believe that the ecological functions provided by secondary forests are buffered against species loss through functional redundancy.

Introduction

Current rates of extinction are estimated to be 100–1000 times greater than rates estimated for pre-human periods (Lawton and May 1995, Pimm et al. 1995). In particular, tropical forests are likely to experience a large reduction in biodiversity should current trends in human activity continue. A major pressure on biodiversity is the destruction of primary tropical forests and their conversion into secondary habitats. The magnitude of loss in biodiversity depends on the ability of these secondary habitats to act as refuges for forest-adapted species. The changes in species diversity due to destruction and conversion of tropical forest are relatively well documented, with most papers reporting a reduction in species diversity. Much less is known about the potential effects of biodiversity loss on ecosystem functions (i.e. energy transformation and cycling of matter), although this might ultimately affect human well-being (Diaz et al. 2006).

Experiments on relatively species-poor assemblages indicate a positive relationship between species diversity and ecological functions (Naeem et al. 1995, McGrady-Steed et al. 1997, Tilman et al. 1997). However, this link is neither close nor universal (Diaz and Cabido 2001, Hooper et al. 2005, Petchey and Gaston 2006). Functional diversity has been defined as "the value and range of those species and organismal traits that influence ecosystem functioning" (Tilman 2001). It is emerging as an important aspect of biodiversity as it determines the strength and shape of the relationship between species diversity and ecosystem functions (Diaz and Cabido 2001). Especially the degree to which species perform similar ecological functions in communities and ecosystems, i.e. the level of functional redundancy, is important for this relationship (Walker 1992, Lawton and Brown 1993). For example, if all species have an equal and additive effect on function (i.e. functional redundancy is low), one might expect a linear relationship between species diversity and the rate of ecosystem processes. If, on the other hand, many species are functionally redundant, the relationship between species diversity and ecosystem processes should become curvilinear. However, the relationship between species diversity and functional diversity in species-rich, natural assemblages is poorly understood (Naeem 2002). To achieve the long-term goal of restoring and managing sustainable ecosystems it is important to understand the linkages and mechanisms between species diversity and ecosystem processes, rather than species diversity as such (Walker 1992). High functional redundancy of species assemblages might indicate that ecosystem functions are robust to changes in diversity. This has important implications for the conservation of biodiversity and ecosystem functions in (regenerating) tropical forests.

A number of methods have been proposed for measuring functional diversity and richness (Tilman 2001, Mason et al. 2005, Petchey and Gaston 2006, Walker et al. 2008). Most ecological research has relied on the number of functional or trophic groups as a measure of functional diversity, though such approaches have disadvantages (Petchey and Gaston 2006). One disadvantage is the disregard for functional differences within organisms of the same group. More recently, measures of functional diversity have been proposed based on the large functional differences that delineate functional groups, as well as the smaller functional differences within these groups (Petchey and Gaston 2006, Walker et al. 2008). Regardless of the method, all measures of functional diversity suffer limitations. For example, the number and type of functional traits together with their correlations might alter the level of functional redundancy which assemblages appear to exhibit (Fonseca and Ganade 2001, Petchey and Gaston 2002b). Thus, research on the relationship between functional and species diversity must also evaluate the sensitivity of results to the functional traits used.

In the present paper we focus on the functional diversity of ant assemblages (Hymenoptera: Formicidae) along a gradient of secondary succession in the Atlantic Forest of Brazil. From a functional perspective, ants play important roles in terrestrial ecosystems. Firstly, ants are unique because of their ubiquity and abundance in terrestrial ecosystems. They constitute 15–20% of the animal biomass in tropical rainforests (Fittkau and Klinge 1973, Wilson 1990) and even more in the forest canopies (Tobin 1994). Secondly, ants interact with their environment by performing a variety of ecological functions. These include their functions as seed dispersers (Beattie 1985, Levey and Byrne 1993), predators (Kaspari 1996a, Philpott and Armbrecht 2006) and ecosystem engineers (Lobry de Bruyn and Conacher 1990, Folgarait 1998). Ants are therefore keystone species in tropical forests, with important ecological functions. In a previous paper we have demonstrated that the taxonomic diversity of ant communities increases with the age of secondary forests in the Atlantic Forest of Brazil (Bihn et al. 2008a). For the same study region, ant behavior at baits indicates an abrupt shift in stoichiometric balances between early and late successional stages of secondary forests, which might affect the functional composition of ant assemblages (Bihn et al. 2008b). Here, we examine the relationship of species diversity to functional diversity of ant assemblages along the same gradient. Specifically, we address the following questions:

(1) What is the relationship between species diversity and functional diversity in ant assemblages of tropical forests? and

(2) How do changes in species diversity along a gradient of regenerating tropical forests affect the functional diversity of ant assemblages?

Methods

Sampling of ants

The study was carried out in the Rio Cachoeira Nature Reserve (25°18’51”S, 48°41'45”W) located near the city of Antonina, in the coastal region of the Brazilian state of Paraná. Dense, ombrophilous lowland and submontane forests originally covered the area, but these suffered intense exploitation and large parts of them had been converted to pastures. The resulting landscape mosaic consists of old-growth forests and secondary forests in various stages of succession (Ferretti and Britez 2006). Between June and September 2003 we sampled leaf litter ants in 12 study sites scattered across the reserve. The sites comprised a chronosequence of four stages of secondary forest succession, with three site replicates for each successional stage: very young secondary forest (4-6 years), young secondary forest (10-15 years), old secondary forest (35-50 years) and old-growth forests (> 100 years). Sites of secondary forests had been used as pastures for buffalo ranching and site age is given as years after abandonment of ranching. Land-use history for study sites was established through interviews with residents and reserve staff corroborated by inspection in a GIS environment of high resolution, geocoded orthophotos from the years 1952, 1980 and 2002. Replicated sites of a particular successional stage were separated by an average distance of 4 km (range: 1–6 km). Replicated sites of a given successional stage were never situated in one continuous patch of the same vegetation type, but separated by areas of different successional stages, pastures, etc. (see Bihn et al. 2008a for a map of the reserve and the location of the study sites within it).

At each study site we established two 50 m transects (parallel, separated by 20 m) and collected leaf litter samples (1 m^2 quadrats) at 5 m intervals along these transects (10 sampling points for each transect). This resulted in 20 samples for each site. Transects were located at least 50 m from any trail, pasture or any other habitat in order to minimize edge effects. Ants were extracted from leaf litter, dead wood and debris collected from the quadrats by sieving through a 1 cm mesh screen and subsequently keeping the sifted material in Winkler bags for 3 days (see Agosti et al. 2000 for a detailed description of the method). All ants were examined and identified by JHB. Many ants had to be assigned to morphospecies because they were undescribed or current systematic knowledge is insufficient to assign valid names. For morphospecies mentioned here, the genus name is followed by an epithet in the form of "JHB00". Otherwise, nomenclature follows Bolton (Bolton 1994; Bolton 2003). Voucher specimens are deposited at the Museu de Zoologia da Universidade de São Paulo, Brazil (MZUSP) and the State Museum of Natural History Karlsruhe, Germany (SMNK).

Southwood (1996) noted that terrestrial insect assemblages are continually challenged by a flow of transient species (also termed tourist, vagrant or occasional species). The proportion of transient species is thought to be high in moist tropical forests (Stevens 1989). For a meaningful analysis one needs to exclude transient species, because these are not biologically associated with the sampled habitat (Magurran and Henderson 2003). Low numbers of individuals and/or low biomass in samples indicate that a species had not established colonies in the (micro)habitat sampled and point to it being transient. Therefore we excluded from all further analysis species which met at least one of the following criteria:

- the number of individuals in all combined samples from a site was less than three and
- the biomass (estimated from the number of individuals and head length with the formula given in Kaspari and Weiser (1999)) of all worker ants from all 20 samples combined was below 0.5 mg (see Figure A in Appendix).

The latter criterion is based on the intuitive idea that resource use of a species is proportional to total biomass. Therefore, the exclusion of species with the lowest biomass leads to assemblages dominated by species with a strong impact on resource use and ecosystem functions. The exact limit of 0.5 mg was arbitrary and mainly motivated by the minimum mass needed for the stable isotope analyses (see below). Additionally, we excluded all army ants (Ecitoninae) from our analysis because their occurrence can not be estimated in a reliable way with the sampling methods employed. We also excluded all males and queens from our analysis because these might never establish colonies after dispersal. This filtering of the original species lists did not qualitatively change the pattern of species richness along the successional gradient (see Figure B in Appendix).

Functional traits

Our intention was to assess the functional diversity of ant assemblages with regard to resource use. Four traits were therefore selected that represent (1) the quantity of resources consumed; (2) the mode of resource acquisition; and (3) the type of resources consumed. The functional traits measured for each species were:

Body size – We used head length as a measure of total body size because of the strong correlation between head length and body mass (Kaspari and Weiser 1999). Body size is generally considered to be one of the most important attributes of an organism because it correlates strongly with many physiological, ecological and life-history traits (Peters 1983). Specifically, the body size of an organism determines the quantity of resources consumed. Head length was measured as the maximum longitudinal length from the most anterior part of the clypeus to the occipital margin, in full face view.

Relative eye size – Larger eyes offer a larger visual field and larger visual overlap of the fields. Ant species with large eyes have excellent vision and are very good at detecting moving objects (Via 1977, Wehner et al. 1983), whereas in ants with reduced eyes, optical cues are of minor importance for orientation and foraging. Eye size is also likely to correlate with the main foraging period (diurnal vs. nocturnal). We measured relative eye size as the ratio of eye length to head length.

Relative leg length – Longer legs allow faster and more efficient locomotion and foraging (Feener et al. 1988, Franks et al. 1999), but also increase their cross-sectional area, which could prevent them from utilizing some foraging niches and types of shelter (Kaspari and Weiser 1999). Thus, relative leg length might yield information about the mode of resource acquisition. Relative leg length was measured as the ratio of leg length (combined length of femur and tibia) to head length.

Trophic position – Most leaf litter ants in tropical forests are thought to be omnivorous and opportunistic feeders, which harvest plant exudates, scavenge and capture live prey as these are encountered (Hölldobler and Wilson 1990). However, for the majority of ant species the relative contribution of different food types to their diet is unknown. The analysis of stable isotope composition of organisms provides an alternative approach to assess their trophic position in food webs (Davidson et al. 2003; Blüthgen et al. 2003). A general result obtained from isotope studies is that consumers have relatively higher $^{15}N/^{14}N$ ratios than their prey. We accordingly used stable isotope data (i.e. $^{15}N/^{14}N$ ratios) to quantify the trophic position of ants.

For the morphological traits (body size, relative eye length, relative leg length) we measured up to five randomly selected (worker) individuals (average: 3.6, range: 3-5 individuals), and used the average of these measurements as the value for each species. In species with distinct minor and major worker castes, we only considered minor workers. Each sample for stable isotope analysis typically contained five workers, but often fewer or more depending on size (range: 2-20 workers). For each species we analyzed one sample for every study site (n = 12) in which it occurred, randomly selecting ant individuals from the leaf litter samples collected at that site. Samples were oven dried at 60°C for 48 h, after removal of the gaster to eliminate the effect of undigested food on isotope measurements. Isotopic N composition of each sample was measured using an elemental analyzer – isotope ratio mass spectrometer (EA-IRMS) coupling (EA type 1108, Carlo Erba, Milano, Italy; ConFlo III interface and gas-IRMS delta S, both Finnigan MAT, Bremen, Germany). The deviation of the sample from the international standard in per mil (‰) is expressed as:

$$\delta^{15}\,\mathrm{N} = [(R_{\mathrm{sample}}/R_{\mathrm{standard}}) - 1] \times 10^3$$

where R_{sample} denotes the ratio between the heavy isotope and its lighter counterpart ($R_{\mathrm{sample}} = {}^{15}\mathrm{N}/{}^{14}\mathrm{N}$) for the sample and R_{standard} the ratio for the international standard (N_2 in the air). N_2 from lecture bottles calibrated against the reference substances N1 and N2 for the N isotopes was used as laboratory standard (Gebauer and Schulze 1991). Reference substances were provided by the International Atomic Energy Agency, Vienna. Acetanilide (Merck, Germany) was used to control the reproducibility and to calibrate N concentration measurements (Gebauer and Schulze 1991).

Species and functional richness and diversity

We calculated functional diversity indices for the ant assemblage in each study site using two widely used indices, following the methods of Petchey and Gaston (functional diversity – FD; Petchey and Gaston 2002b, Petchey and Gaston 2006) and Walker et al. (functional attribute diversity – FAD; Walker et al. 1999). For the computation of FD, the species by trait matrix was converted into a distance matrix and this was clustered to produce a dendrogram. We used z-standardized values to assign all functional traits equal importance in our analysis. The FD of an assemblage is defined as the combined length of all branches in this dendrogram. The choice of distance and clustering method for the calculation of FD may greatly affect the FD values. Thus, we followed the approach proposed by Mouchet et al. (2008) and tested several distance and clustering methods (including consensus trees), and then selected the most reliable tree for the calculation of FD based on the cophenetic correlation between pairwise distances in trait space and pairwise distances across the dendrogram (see Mouchet et al. 2008 for the distance and clustering algorithms used and details of the method). The combination of Euclidean distances and the unweighted pair group centroid method (UPGMA) yielded the strongest cophenetic correlation (0.85) and was used throughout our analysis. The FAD of an assemblage is the total of all pairwise distances between species in functional trait space. Again, we used Euclidean distances as a measure of dissimilarity.

In their original form, both indices of functional diversity weight every species in a given assemblage equally, i.e. they do not take into account the relative abundance of species. These unweighted indices are therefore a measure of functional richness. For exploration of the relationship between functional richness and species richness we used the (unweighted) FD index and the observed species richness per site. For the calculation of functional and species diversity we applied occurrence-based rarefaction (see below) to the FD index and species richness. This resulted in indices which account for evenness in species assemblages. The contribution of each species of an assemblage is weighted by its relative number of occurrences per site, i.e. the number of samples (n=20) per site in which it was recorded.

We plotted values of functional richness and diversity against species richness and diversity and tested for saturation using multiple regression with species richness and quadratic species richness as predictor variables. The analysis was repeated for the relationship between species and functional richness using different combinations of only three of the four functional traits, to evaluate whether our results were robust with respect to the number and combination of functional traits considered.

Functional diversity during forest succession

For the comparison of functional diversity indices among ant assemblages we followed the functional rarefaction method as proposed by Walker et al. (2008). This transforms the unweighted indices FD and FAD into unbiased weighted indices, where each index is weighted by the frequency of occurrence of each species in the assemblage. Because the number of species occurrences varied from site to site (range: 59 – 282), occurrence- based rarefaction was required for the comparison of functional and species diversity among sites. We estimated <S_n>, <FAD_n> and <FD_n> for n = 2 and 59 occurrences and make use of the following three properties of the calculated indices for the interpretation of the results (Walker et al. 2008). First, the functional diversity indices FAD and FD are sensitive to the differences in the functional traits of species whereas the indices of species diversity <S_2> and <S_{59}> are not. Second, the rarefaction to different numbers of occurrences gives way to the evaluation of the sensitivity to rare species. <S_{59}>, <FAD_{59}> and <FD_{59}> are more sensitive to rare species than <S_2> and <FAD_2>. Third, Petchey and Gaston (2006) emphasize that FD is insensitive to functionally redundant species whereas <FAD_2>, <FAD_{59}>, <S_2> and <S_{59}> are sensitive to these.

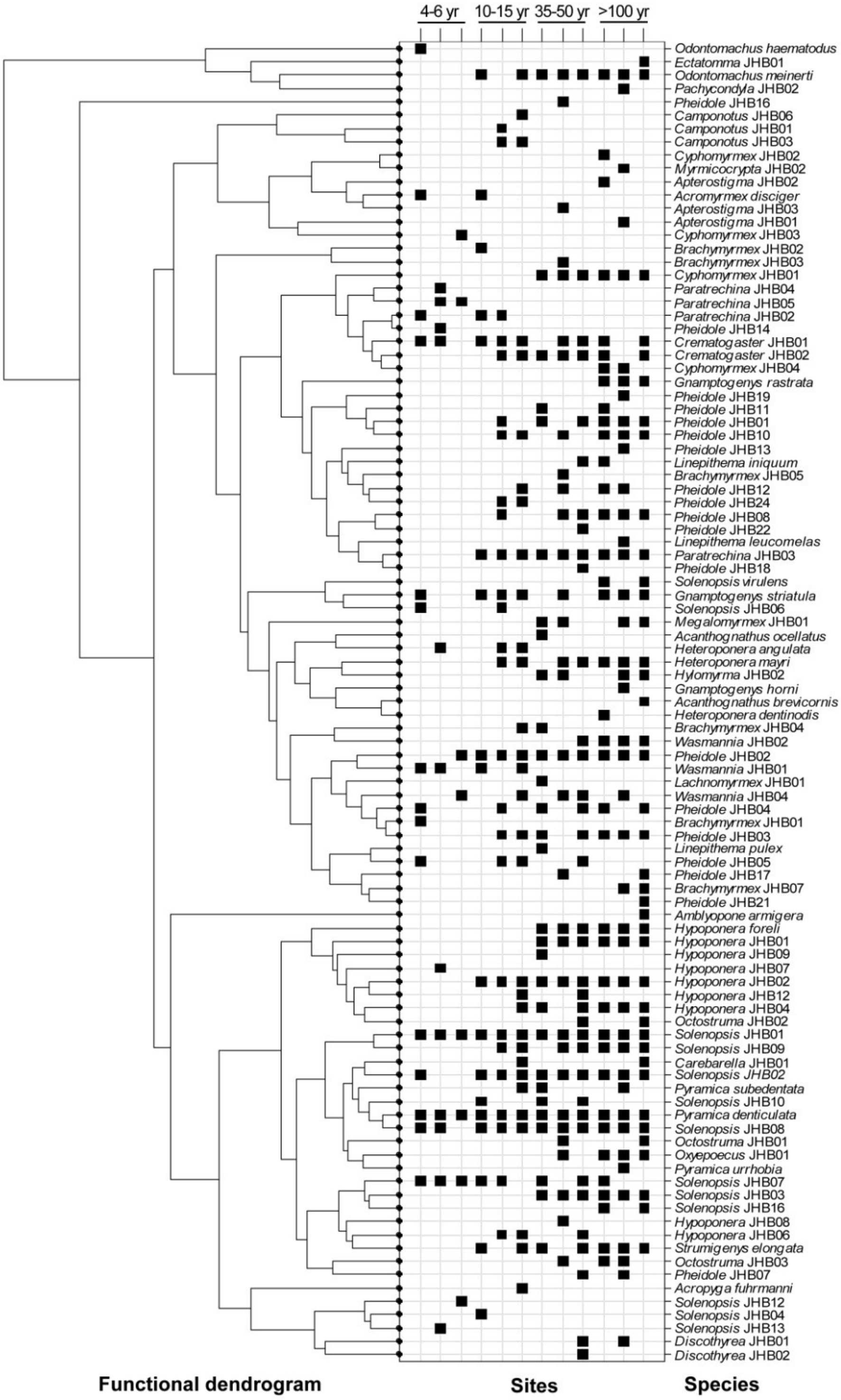

Figure 1. Summary of the data set. On the right: a representation of the species occurrence matrix with species as rows and sites as columns. Sites are grouped by successional stage and ordered from left to right by increasing time since abandonment of use as pastures. A black square indicates the presence of a species. On the left: the functional relationship among 99 ant species that were sampled at the Rio Cachoeira Nature Reserve. The dendrogram was produced by hierarchical clustering with the UPGMA algorithm of the Euclidean distance matrix calculated from the standardized functional traits of species.

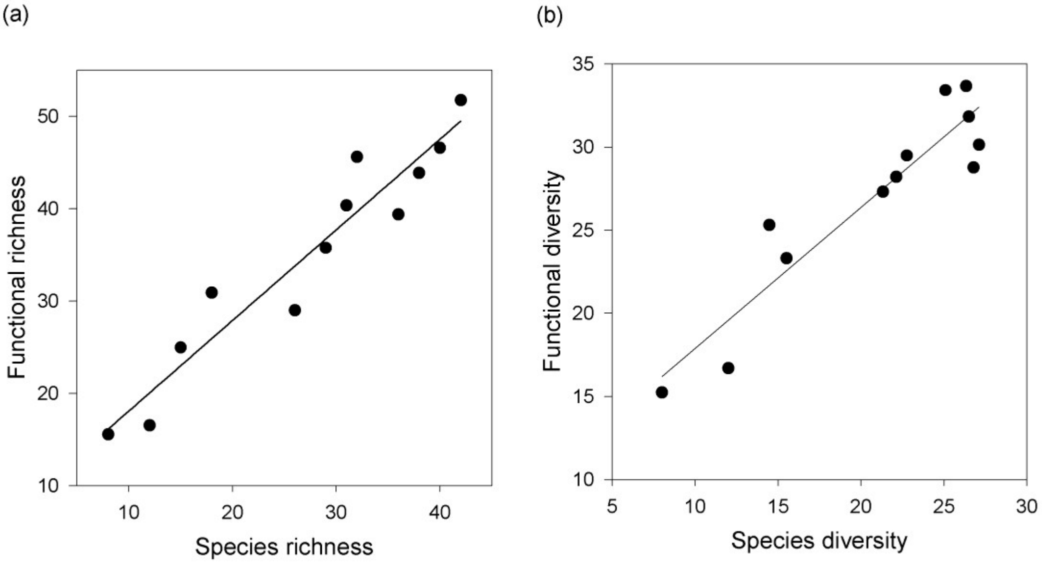

Figure 2. Relationship between functional and species richness (a) and functional and species diversity (b) across 12 ant assemblages sampled at Rio Cachoeira Nature Reserve, Brazil.

We found a linear relationship between functional richness and species richness and between functional diversity and species diversity (Fig. 2). For both relationships, the effect of squared species richness was not significant in the multiple regression model (richness: $P = 0.79$; diversity: $P = 0.21$). This indicates that linear regression is an appropriate way to describe the relationships. There was a close, linear relationship between species and functional richness ($r^2 = 0.92$; $P < 0.001$; Fig. 2a) and species and functional diversity ($r^2 = 0.87$, $P < 0.001$; Fig. 2b). These results proved robust to use of different numbers and combinations of functional traits (Fig. 3). The amount of variation explained by the relationship between species and functional richness was similar in all cases (all traits: $r^2 = 0.92$; without trophic position: $r^2 = 0.92$; without relative eye size: $r^2 = 0.85$; without body size: $r^2 = 0.92$; without relative leg length: $r^2 = 0.93$). The increase in functional richness with increasing species richness was not influenced by the number and combination of functional traits (ANCOVA: $P = 0.97$).

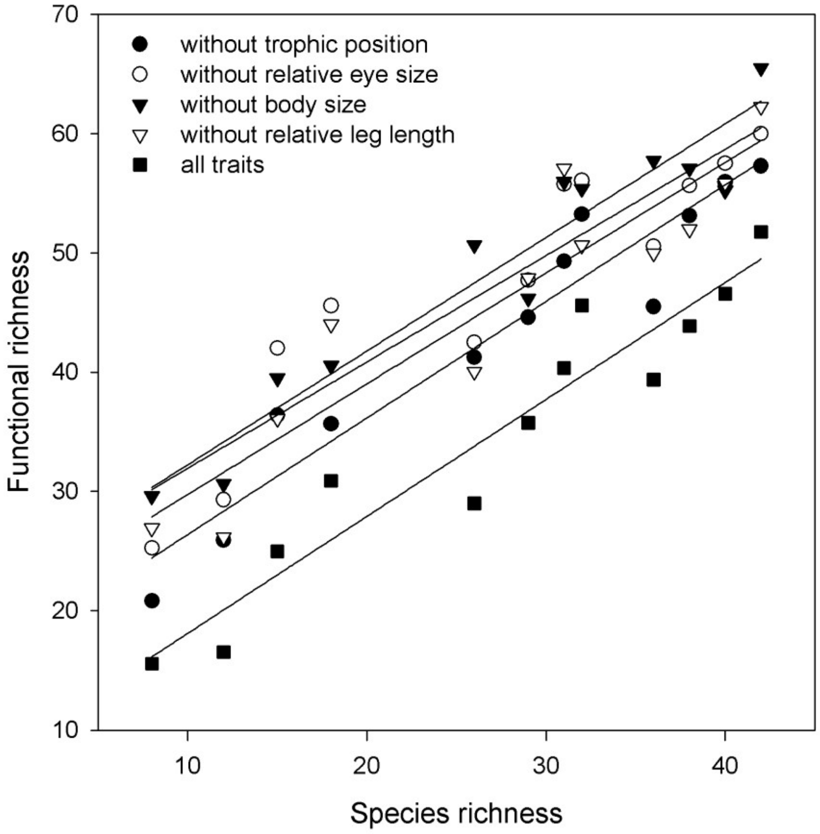

Figure 3. Relationship between species and functional richness for different sets of functional traits. The traits used for the calculation of functional richness were body size, relative leg length, relative eye size and trophic position. Each point represents the function and species richness for an ant assemblage using all four traits and all combinations of only three of these traits.

We found increasing values for the indices <S_2>, <S_{59}>, <FAD_{59}> and <FD_{59}> along the successional gradient (ANOVA, linear trend: <S_2>: $F_{1,8}$ = 26.01, $P < 0.001$; <S_{59}>: $F_{1,8}$ = 47.29, $P < 0.001$; <FAD_{59}>: $F_{1,8}$ = 44.79, $P < 0.001$; <FD_{59}>: $F_{1,8}$ = 19.12, $P = 0.002$; Fig. 4). <FAD_2> did not show a clear pattern among the successional stages (ANOVA, linear trend: $F_{1,8}$ = 0.41, $P < 0.54$). Because of the complementary properties of the employed indices, we can make several conclusions based on the observed pattern:

- <S_2> and <S_{95}> increased with successional age. Thus, species diversity of leaf litter ants increased along the successional gradient.
- Functional diversity of ant assemblages also increased with increasing successional age, and species that are recruited to assemblages are likely to be

unique with respect to their functional traits. Two out of three indices of functional diversity, including <FD_{59}>, which is insensitive to functionally redundant species, increased along the successional gradient.

- The recruitment of rare species was largely responsible for the increase in functional diversity of ant assemblages. Though some common species became more abundant over time (<S_2> significantly increased), we did not detect a significant increase in the functional differences among common species (as measured by <FAD_2>). This suggests that the common species which became more abundant along the successional gradient were not sufficiently unique with respect to their functional traits to result in significant increase in <FAD_2> and that the increase in <FAD_{59}> resulted from functionally unique rare species.

Discussion

The relationship between species and functional diversity is still poorly documented for most ecological systems (Naeem 2002). We show here that functional richness and diversity are closely related to species richness and diversity, and that functional redundancy is low among coexisting species of tropical leaf litter ants. The link between species diversity and functional diversity is strong and positive for the entire range of local species richness, with no evidence for saturation in this relationship. Recovery of species richness and diversity of ant assemblages in tropical secondary forests were accompanied by an increased functional richness and diversity of assemblages. Moreover, our results indicated that the increase in functional diversity along the successional gradient of secondary forests is primarily driven by rare species which are functionally unique. The decline in ant species diversity in tropical forests due to human alteration of the environment is likely to result in a proportional decline of the ecological functions performed by this keystone taxon.

The observed level of functional redundancy might depend on the number of traits used for the measurement of functional richness and diversity (Fonseca and Ganade 2001, Petchey and Gaston 2002b). The inclusion of a large number of uncorrelated functional traits will inevitably produce assemblages with low functional redundancy. Thus, traits need to be selected with care. Experimental evidence of their functional significance would be the best approach for their selection (Petchey and Gaston 2006). Nevertheless, the traits used in our study are widely recognized as being associated with differences in resource use among ant species (Kaspari 1996b, Gotelli and Ellison 2002, Davidson et al. 2003, Blüthgen et al. 2003). Weiser and Kaspari (2006) demonstrate that body size, relative leg length and relative eye size explain most of the variation in ecological morphospace among ant species of the New World and that these traits are linked to the foraging behavior of ants. The rather modest number of traits used in our study compared to other studies on patterns of functional diversity therefore does not seem problematic. Most importantly, even when we repeated our analysis with only three traits, a similar relationship between species and functional richness emerged (Fig. 3). Thus, our conservative approach with respect to the number of included functional traits revealed patterns of low functional redundancy consistent with our results for the full set of traits.

Our results allow predictions to be made about the potential gains and losses in functional diversity associated with community assembly during secondary succession. The analysis suggests that small changes in species diversity can have rather large effects on functional diversity, and possibly ecosystem functioning, within a community. Therefore, the conservation of a large proportion of the ecological functions of communities requires the conservation of a large proportion of the species that make up the community. Moreover, our results suggest that rare species often possess unique combinations of functional traits. Since rare species are especially prone to extinction (Gaston 1994), anthropogenic disturbances could lead to rapid loss of ecosystem functions performed by these species.

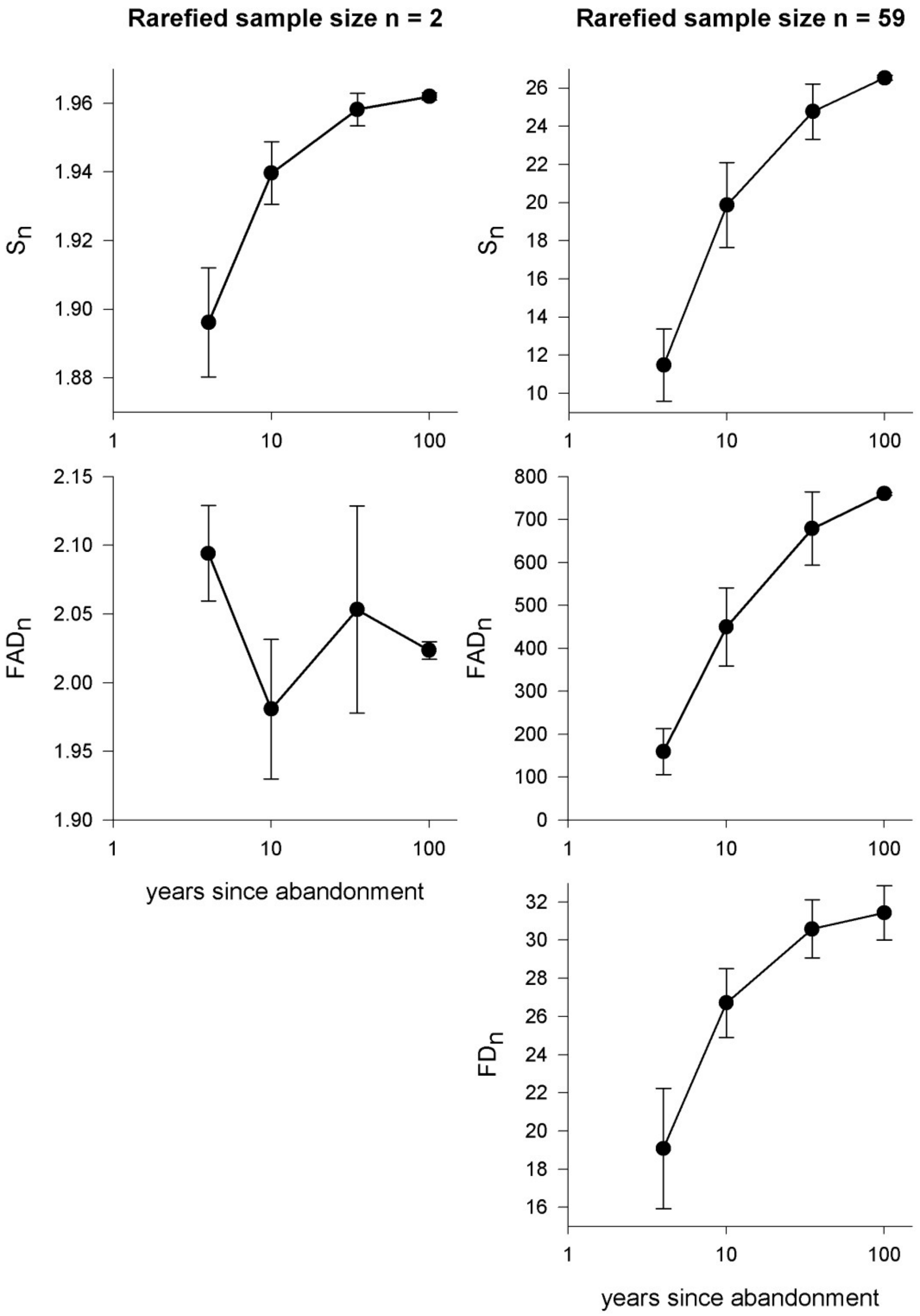

Figure 4. Changes in the functional and species diversity of leaf litter ant assemblages in the Rio Cachoeira Nature Reserve along a gradient of forest succession. Five diversity indices are used: $\langle S_2 \rangle$, $\langle S_{59} \rangle$, $\langle FD_2 \rangle$, $\langle FAD_{59} \rangle$ and $\langle FD_{59} \rangle$. Dots and error bars are means of estimated levels of diversity with standard errors for each successional stage (n = 3).

The recovery of species and functional diversity followed similar trajectories through secondary succession (Fig. 4). Both measures of biodiversity were closely related and increased monotonically with increasing age of secondary forests. Nevertheless, it may take many decades until species and functional diversity reach levels similar to those in primary forests. For conservation practice this means that the largest possible range of functional traits and probably also ecosystem functions can only be preserved in primary forests. Our results also suggest that classical measures of biodiversity such as species richness and diversity might be good surrogates for functional richness and diversity of communities. The monitoring of the diversity of invertebrates is often time-consuming and costly. This is especially true for tropical ecosystems where many invertebrate taxa are hyperdiverse. The assessment of functional diversity of invertebrate assemblages will in most cases involve the measurement of a set of functional traits of species, which puts even more strain on resources of time and money. As long as species diversity explains much of the variation in functional diversity, as suggested by our study, the measurement of functional traits is not necessary. The conservation of local species diversity will result in the conservation of an almost proportional amount of ecological functions. At this time, however, it would be premature to draw final conclusions based on our particular system. Indeed, our study is one of the first which explores the relationship between species and functional diversity for a species-rich assemblage of invertebrates in the tropics. Based on the results of simulated random extinctions of species in a South American plant community, Fonseca and Ganade (2001) conclude that as much as 75% of the species can be lost before changes in the functional diversity (measured as functional group richness) become evident. This seems to be not the case in our study. Differences between their findings and ours could result from different measures of functional diversity used in the studies (number of functional groups in the study of Fonseca and Ganade 2001), which make comparison difficult. Concordant with our results, Michel and Halpern (2005) report a strong positive relationship between species and functional diversity, and increased functional diversity coinciding with the recovery of species richness in marine reserves. A similar linear relationship was also found in a study simulating the random extinction of species from five animal and plant assemblages (Petchey and Gaston 2002a). In contrast, Ernst et al. (2006) demonstrate that functional diversity of tropical amphibian communities in secondary forest is lower than in primary forests but that this reduction in functional diversity does not always match patterns of species diversity, indicating a rather loose relationship between these two measures of biodiversity. These contradicting results for different taxa and environments highlight the urgent need for studies on the consequences of human actions on the pattern of functional diversity in natural assemblages.

Further studies should also clarify how changes in the functional diversity of natural assemblages impact ecosystem functioning. Our study does not provide a direct link between species diversity and ecosystem functioning and the observed changes in functional diversity might not proportionally translate into changes of any single ecosystem function. The majority of studies on the effect of biodiversity on ecosystem functioning has used synthetically assembled communities and measured the effect of changes in species composition on single ecosystem process rates or properties. Equating single functions with overall functioning may ignore other important ecosystem processes and can be highly misleading (Rosenfeld 2002, Gamfeldt et al. 2008). Our approach might better reflect the multiple ecological functions species provide in ecosystems and avoid the bias towards detecting ecological redundancy by focusing on a single ecological function.

Management and conservation of tropical forests will require a better understanding of the value of secondary forests for biodiversity conservation. Invertebrates provide essential ecological functions in most ecosystems (Wilson 1987). For most invertebrate groups we lack information about the extent to which secondary forests can preserve even relatively simple aspects of biodiversity such as species richness and diversity. In the long term, the link between ecological functions and species diversity might have very important effects on the complex interactions affecting human well-being. Our results offer a first insight into the nature of these relationships in species-rich assemblages of tropical forests. The low functional redundancy among species in our study indicates that species loss due to human alteration of the environment will lead to a severe decline in ecological functions. Therefore, secondary forests might not only harbor much reduced species diversity but also offer significantly reduced ecosystem functions in comparison to undisturbed forests. More studies on the functional diversity of assemblages in secondary forests and their impact on ecological functions are needed to provide guidance for the conservation and restoration of tropical forest communities.

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4 Community assembly of tropical ants: body size and trophic niche

with Gerhard Gebauer and Roland Brandl
in preparation

Abstract

Understanding the processes that lead to the assembly of local communities from the regional species pool is a major endeavor in community ecology and will strengthen biodiversity conservation efforts. To date, relatively little is known about the community assembly of invertebrates in tropical forests, though they constitute a major part of biodiversity. This is why we focus in this study on the community assembly of tropical leaf litter ants in the Atlantic Forest of Brazil. Ants were sampled from 240 one-square-meter quadrats. We tested for non-random patterns in niche space occupation, comparing observed patterns with expected patterns based on two null models. The niche space of local ant communities was defined by body size and trophic position of coexisting species. We characterized niche space by estimating the total space occupied and calculated mean nearest neighbor distances between species. Additionally, we tested for significant changes in the pattern of niche space occupation along a successional gradient of forests. The recruitment of additional species to the niche space occupied by resident species resulted primarily in tighter species packing and secondarily in an increase of total niche space. These results indicate that local ant communities are assembled from the regional species pool mainly through non-interactive processes. Despite marked differences in species richness and composition, the pattern of niche space occupation was relatively constant along the successional gradient. This suggests that favorable resource availability and habitat conditions, rather than competition, are the major force structuring tropical leaf litter ant communties. If this is true, the regeneration of local species richness during secondary forest succession in the tropics is primarily a product of the suitability of the local environment for species adapted to it.

Introduction

The search for processes that structure species communities is still an active area of ecology (Lawton 1999; Weiher and Keddy 1999). The question of how communities come together dates back to the early disputes on plant succession (Clements 1938; Gleason 1927). In animal ecology, it was Diamond`s influential work (Diamond 1975) on the assembly of bird communities which stimulated a flush of studies and discussions (e.g. papers in Strong et al. 1984). These discussions converged to the view that the assembly of communities depends on the regional species pool and is therefore contingent upon the organisms involved, and on the historical and biogeographical context (Lawton 1999; Ricklefs and Schluter 1993). Within smaller areas and over ecological time scales local processes, such as competition, predation and environmental variability enter the overall equation of species coexistence. The theoretical framework of interspecific competition predicts that within communities species should differ in their ecological traits and functions to reduce overlap in resource use and allow for species coexistence (Gotelli and Ellison 2002; MacArthur and Levins 1967).

One way to study community assembly is to analyze the distribution of coexisting species in *niche space* — the *n*-dimensional envelope containing all the niches present in a community. In this paper, we examine the assembly of communities of tropical leaf litter ants (Hymenoptera: Formicidae) and analyze the distribution of coexisting species in a niche space defined by body size and trophic position. This type of analysis of biological communities in hyperdimensional space defined by ecological or morphological traits played an essential role in our understanding of evolutionary patterns in the fossil record (Foote 1997). In ecology, such analyses have been applied to the question on how species are added to communities. Critical to the understanding of the relative influence of local processes are the mechanisms by which changes in species richness are accommodated within the niche space of local communities (Ricklefs and Schluter 1993). Two alternative models have been suggested in which the distribution of species in niche space changes when the number of species in local communties increases (Ricklefs and Miles 1994):

- *The space-increasing mechanism*: New species are preferentially added to the periphery of the niche space occupied by resident species. This should result in a larger total niche space while the interspecific distances between species in niche space will remain constant. This pattern is consistent with the operation of competitive interactions where species differ in their functional traits to reduce overlap in resource use.

- *The species packing mechanism*: New species are inserted within the niche space already established by resident species. In this case, the interspecific distances in niche space should decrease with an increase in species richness. This pattern points to a minor influence of competition on community assembly and indicates a larger influence of environmental filters on community composition (Weiher and Keddy 1995). Coexisting species are more similar to one another than would be expected by chance, reflecting shared ecological tolerances.

Vertebrate communities are often assembled according to the space-increasing mechanism (reviewed in Ricklefs and Miles 1994). This pattern was also found in a comparison of the morphological space occupied by temperate and tropical communities of moths (Ricklefs and O´Rourke 1974). The greater species richness in tropical communities was correlated with greater diversity in form. In other types of communities, increased species packing is the dominant mechanism by which the addition of species is accommodated in niche space. For example, the total niche space of herbivorous insects on bracken varies independently of species richness (Lawton et al. 1993).

By definition, succession leads to changes in species interactions over time. In a qualitative model, Weiher and Keddy (1995) proposed a predictable shift in the mechanisms of community assembly along a gradient of disturbance or abiotic stress. Under high environmental adversity communities should assemble according to the species packing mechanism. Conversely, under low levels of environmental adversity the space-increasing mechanism will be more important for community assembly. For forest adapted species, like leaf litter ants, environmental adversity should decrease from early successional stages to late successional stages and thus result in different assembly mechanisms along a gradient forest succession.

Ants are an ideal taxon for testing patterns of community assembly because competition is generally regarded as an important structuring force on ant communties (Andersen 1992; Levings and Traniello 1981; Savolainen and Vepsäläinen 1988; Morrison 1996; Hölldobler and Wilson 1990). Our study investigates the assembly of leaf litter ant communities along a successional gradient in the Atlantic forest of Southern Brazil. Local processes, such as competition, can only be measured when species are able to interact in ecological time. The basic unit of our study is therefore 1 m^2 – a spatial scale which allows all ants living within to potentially interact. Specifically, we test the following predictions:

(1) As more species are recruited to local communities, the total niche space occupied by coexisting ant species will increase because new species are preferentially added to the periphery of the space already occupied.

(2) The relative strength of different assembly mechanism changes along the successional gradient. In early stages of forest succession, ant communities are assembled according to the species packing mechanism. In late successional stages, patterns of niche space occupancy are concordant with the space-increasing mechanism.

Methods

Sampling of ant communities

The study was carried out in the Rio Cachoeira Nature Reserve (25°18’51”S, 48°41'45”W) located near the city of Antonina, in the coastal region of the Brazilian state of Paraná. The regional climate is classified as Köppen’s Cfa, or mesothermic subtropical humid. Dense, ombrophilous lowland and submontane forests originally covered the area, but these suffered intense exploitation and large parts of them had been converted to pastures. The resulting landscape mosaic consists of old-growth forests and secondary forests in various stages of succession.

Between June and September 2003 we sampled leaf litter ants in 240 one-square-meter quadrats distributed among 12 sites scattered across the reserve. The sites comprised a chronosequence of four stages of secondary forest succession, with three replicated sites for each successional stage: very young secondary forest (4-6 years), young secondary forest (10-15 years), old secondary forest (35-50 years) and old-growth forests (> 100 years). Sites of secondary forests had been used as pastures for buffalo ranching and site age is given as years after abandonment of ranching. Land-use history for study sites was established through interviews with residents and reserve staff and corroborated by inspection in a GIS environment of high resolution, geocoded orthophotos from the years 1952, 1980 and 2002. Replicated sites of a particular successional stage were separated by an average distance of 4 km (range: 1-6 km). Replicated sites of a given successional stage were never situated in one continuous patch of the same vegetation type, but separated by areas of different successional stages, pastures, etc.

(see Bihn et al. 2008a for a map of the reserve and the location of the study sites within it).

The basic sampling units of this study were 1 m^2 quadrats. At each study site we established two 50 m transects (parallel, separated by 20 m) and collected leaf litter samples (1 m^2) at 5 m intervals along these transects (10 sampling points for each transect). This resulted in 20 samples for each site. Transects were located at least 50 m from any trail, pasture or any other habitat in order to minimize edge effects. Ants were extracted from leaf litter, dead wood and debris collected from the quadrats by sieving through a 1 cm mesh screen and subsequently keeping the sifted material in Winkler bags for 3 days. The short foraging range of most leaf litter ants in tropical forests (Byrne 1994) probably resulted in negligible overlap of colonies among samples. All ants were examined and identified by JHB. Many ants had to be assigned to morphospecies because they were either undescribed or current systematic knowledge is insufficient to assign valid names. For morphospecies mentioned here, the genus name is followed by an epithet in the form of “JHB00”. Otherwise nomenclature follows Bolton (Bolton 1994;Bolton 2003). Voucher specimens are deposited at the Museu de Zoologia da Universidade de São Paulo (MZUSP) and the State Museum of Natural History Karlsruhe (SMNK).

For a meaningful analysis of community assembly one needs to exclude transient species (also termed tourist, vagrant or occasional species), because these have little impact on local interactions (Magurran and Henderson 2003). Low numbers of individuals in samples indicate that a species had not established colonies in the (micro)habitat sampled and points to it being transient. Therefore we excluded from all further analysis species which met at least one of the following criteria:

- the number of individuals in all combined samples of a site was less than three and
- the biomass (estimated from the number of individuals and head length with the formula given in (Kaspari and Weiser 1999) of all worker ants from all 20 samples combined was below 0.5 mg (see Figure A in Appendix).

The latter criterion is based on the intuitive ideas that resource use is proportional to total biomass of a species. Therefore, the exclusion of species with the lowest biomass could produce communties which are biased towards finding strong interspecific interaction among coexisting species. The exact limit of 0.5 mg was arbitrary and mainly motivated by the minimum mass needed for the stable isotope analyses (see below). Additionally, we excluded all army ants (Ecitoninae) from our analysis because their occurrence cannot be estimated in a reliable way with the sampling methods employed. We also excluded all males and queens from our analysis because immigrated single queens might never rear workers and establish colonies. This filtering of the original species lists did not qualitatively change the pattern of species richness along the successional gradient (see Figure B in Appendix).

Functional traits

A functional trait is a trait that influences performance and resource use. We used two important functional traits in our analysis: body size and trophic position (as measured by δ^{15} N), which reflect much of the resource use of organisms. Body size is generally considered to be one of the most important attributes of an organism because it correlates strongly with many physiological, ecological and life-history traits (Peters 1983). The size of organisms has also a large influence on community structure and function (Yodzis and Innes 1992). Diet influences population densities and consequently community structure of ants (Hölldobler and Wilson 1990). Most leaf litter ants in tropical forests are thought to be omnivorous and opportunistic feeders, which harvest plant exudates, scavenge and capture live prey. For the vast majority of ant species, however, the mode of nutrient acquisition and relative contribution of different food types to their diet is unknown. The analysis of stable isotope composition of organisms provides an approach to assess their trophic position in food webs (Blüthgen et al. 2003; Davidson et al. 2003).

We used head length as a measure of total body size because of the strong correlation between head length and body mass (Kaspari and Weiser 1999). Head length was measured as the maximum longitudinal length from the most anterior part of the clypeus to the occipital margin in full face view. For each species we measured head length on up to five randomly selected (worker) individuals (average: 3.6, range: 3-5 individuals), and we used the average of these measurements as the value for each species. In species with minor and major worker castes, we only considered minor workers.

Each sample for stable isotope analysis typically contained five workers, but often fewer or more depending on size (range: 2-20 workers). For each species we analyzed one sample for every study site (n = 12) in which it occurred, randomly selecting ant individuals from the samples collected at that site. Samples were oven dried at 60° C for 48 h, after removal of the gaster to eliminate the effect of undigested food on isotope measurements (Blüthgen et al. 2003). Samples were weighted on an electronic balance (Sartorius M25D, Göttingen, Germany). Isotopic N composition of each sample was measured using an elemental analyzer – isotope ratio mass spectrometer (EA-IRMS) coupling (EA type 1108, Carlo Erba, Milano, Italy; ConFlo III interface and gas-IRMS delta S, both Finnigan MAT, Bremen, Germany). The deviation of the sample from the international standard in per mil (‰) is expressed as:

$$\delta^{15}\,N = [(R_{sample}/R_{standard}) - 1] \times 10^3$$

where R_{sample} denotes the ratio between the heavy isotope and its lighter counterpart ($R_{sample} = {}^{15}N/{}^{14}N$) for the sample and $R_{standard}$ the ratio for the international standard (N_2 in the air). N2 from lecture bottles calibrated against the reference substances N1 and N2 for the N isotopes was used as laboratory standard (Gebauer and Schulze 1991). Reference substances were provided by the International Atomic Energy Agency, Vienna. Acetanilide (Merck, Germany)
was used to control the reproducibility and to calibrate N concentration measurements (Gebauer and Schulze 1991).

Analyses are based on the position of each species of a community (from 1 m^2 quadrats) in two-dimensional niche space, the axes of which are the z-standardized values of the two variables: body size and trophic position. We used z-standardized values to give both functional traits equal importance in our analysis.

Community assembly

We tested the generalization about the relationship of species richness and functional similarity proposed by Ricklefs and Schluter (1993), by computing interspecific distances among coexisting species and the total space occupied in niche space. For the quantification of interspecific distances between coexisiting species, we determined the mean nearest-neighbor distance (mNND). mNND is calculated as the mean of Euclidean distances of each species' nearest neighbor in niche space and thus a measure of the density of species packing. We used the convex hull area (CHA; Cornwell et al. 2006) to quantify the total space occupied by coexisting species. We excluded ten samples with less than three species because the calculation of CHA is meaningless in two species communities. Therefore, all analysis involving the calculation of CHA and mNND are based on 230 samples. We analyzed the relationship between species richness and mNND, and between species richness and CHA by comparison to expected values from null models. We plotted the observed values vs. the expected values for simulated communities with the same number of species. Observed values (CHA and mNND) were $\log_{10}$-transformed and compared to means of the $\log_{10}$ values from simulations. We calculated the slope (± 95% confidence intervals) for linear relationships between observed and expected values based on major axis regression. CHA and mNND were calculated with R, Version 2.4.0 (http://www.r-project.org). Major axis regressions were calculated with the smatr package (ver. 2.1; Warton et al. 2006) for R.

Null models

We used two different null models to derive the expected niche space occupation in communities drawn randomly from the regional species pool (i.e. all species sampled): an equiprobable source pool model and an occurrence-weighted source pool model. In the equiprobable source-pool model, species are drawn randomly and with equal probability from the regional species pool. Foundress queens of many ant species can fly great distances and disperse widely from their nests (Hölldobler and Wilson 1990). From this and in combination with the relatively small size of the reserve and the mosaic nature of the vegetation types, species may be able to disperse to any of our study sites. Alternatively, the colonization of different successional stages might be limited to a subset of species with certain functional characteristics. Species, which exploit rare resources, might be coupled to the distribution of these resources. For example, many tropical ant species live in obligatory mutualism with plants and these plants could be limited in their distribution to early or late successional stages of forest regeneration. Therefore, we also used an occurrence-weighted source-pool model, in which the probability of drawing a particular species is proportional to the number of samples in which that species occurred in the regional pool (i.e. the total number of samples in which it was detected). For each null-model we constructed 10 000 simulated communities for each observed value of species richness and calculated the mean and variance. Calculations were done with custom written scripts in R.

Effects of succession on community assembly

For the comparison of results across successional stages, we calculated the standard effect size (SES), which measures the number of standard deviations that each of the observed measures of trait dispersion in niche space is above or below the mean of that measure for the simulated null communities:

$$SES = (D_{obs} - D_{sim})/SD_{sim}$$

D_{obs} corresponds to the index (CHA or mNND) for the observed community, D_{sim} corresponds to the index for the simulated community, and SD_{sim} is the standard deviation for the simulated community. For each site we calculated the mean SES for the CHA and mNND and tested for significant differences in SES among successional stages with a single factor ANOVA.

Results

Niche space of ants

Our analysis was based on the distribution of 99 species (30 genera) in 230 local communities. Species richness for 1 m^2 quadrats ranged from 2 to 22 species (mean 9.2 ± 0.3 SE). Ant species covered a wide range of body sizes and trophic positions (Fig. 1). The mean head length of the smallest ant (0.34 mm; *Brachymyrmex* JHB02) was almost eight times smaller than that of the largest ant (2.67 mm; *Odontomachus haematodus* (L. 1758). Mean δ^{15} N values ranged from 1.94 (*Acropyga fuhrmanni* (Forel 1914) to 10.8 (*Amblyopone armigera* Mayr 1887) with a mean value of 6.77 (±0.18 SE) across all species. Body size and trophic position were not correlated ($r = 0.06$, $p = 0.57$). The rarity of species is linked to their distribution in niche space (Fig. 1, inset). Rare species tended to occupy more peripheral positions in niche space relative to common species.

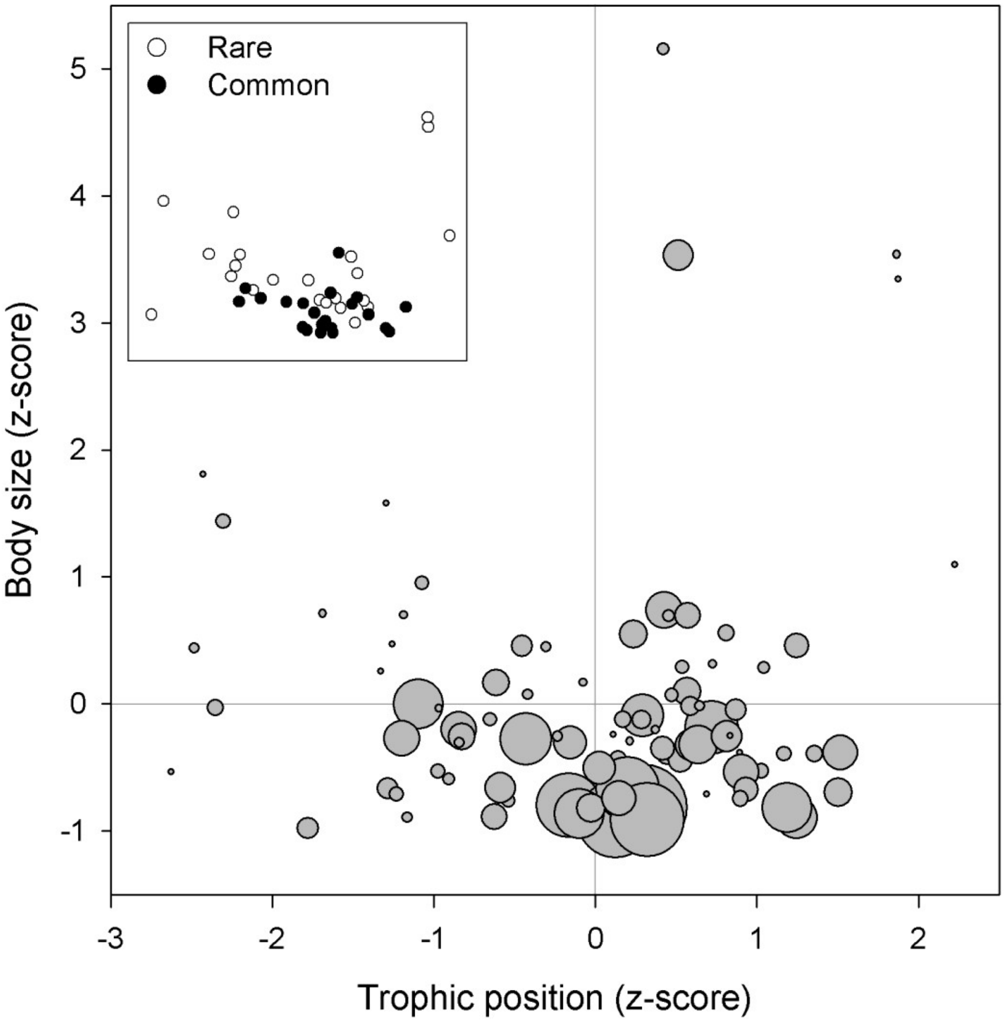


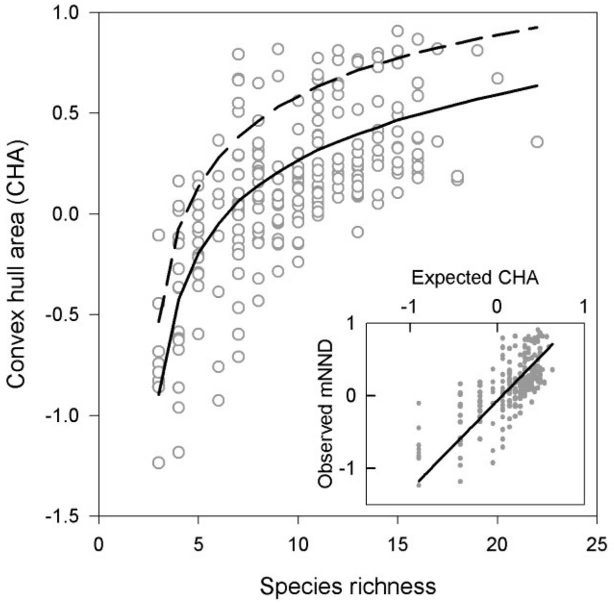
Figure 1: The distribution of ant species in niche space as defined by body size and trophic position. Species` number of occurrences in samples is indicated by the relative size of the circles. Inset shows the distribution of the 22 rarest species (one or two occurrences in 240 samples) vs. the distribution of the 22 most common species (more than 30 occurrences in 240 samples) in niche space.

Community assembly

The observed and simulated size of the occupied niche space (CHA) as well as species packing (mNND) increased with species richness (Fig. 2). Cumulatively, across all real ant communities, the spread of functional traits was significantly lower than expected from the null-models (paired t-test: $p < 0.05$ for both null models). The slopes for the relationship between observed CHA and expected CHA were significantly larger than 1. The slope (major axis regression) of observed vs. expected CHA from the equiprobable null model was 1.41 (95% CI:

1.24 – 1.61); the slope of observed vs. expected CHA from the occurrence-weighted null model was 1.33 (95% CI: 1.18-1.52). This implies that the increase of niche space with species richness was larger than expected by chance.

a) Convex hull area



b) Mean nearest neighbor distance

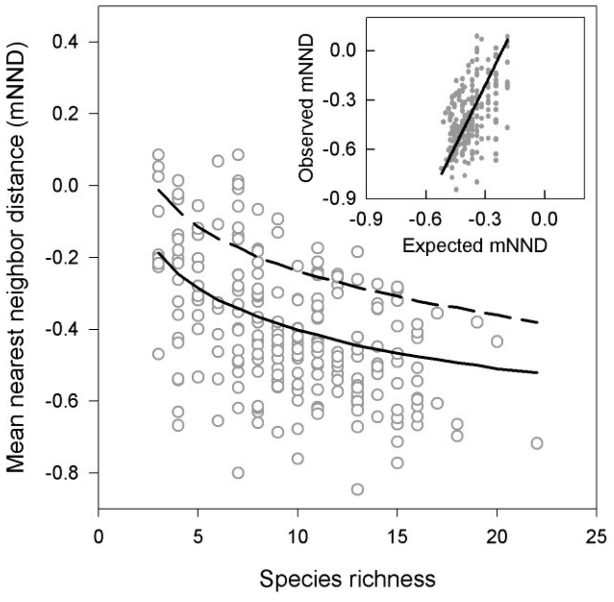


Figure 2: The relationship between species richness and two different metrics of niche space occupation of ant communities for each one m^2 sample (n = 230); (a) convex hull area (CHA), representing the total niche space occupied; (b) mean nearest neighbor distance (mNND), reflecting species packing in niche space. Lines are the mean of random communities calculated for the equiprobable null model (dashed line) and occurrence weighted null model (solid line). Insets show observed vs. expected CHA or mNND from simulation based on the occurrence-weighted null model. Lines are fitted lines from major axis regression.

The mean nearest neighbor distance of ant communities in niche space decreased with increasing number of species in communties (Fig. 2b). Across all ant communities, mNND was lower than expected from simulated communities based on the equiprobable null model (paired t-test: $p < 0.01$), marginally significant in comparison to random communities generated with the occurrence weighted null model ($p = 0.08$). As species richness of ant communities increased, the decrease of mNND was stronger than would have been expected from random communities: equiprobable null model: slope (major axis regression) = 3.87 (95% CI: 3.16-4.94); occurrence weighted null model: slope (major axis regression) = 4.22 (95% CI: 3.45-4.94). This suggests that species packing is higher than expected as more species are added to the communities.

Community assembly during succession

An analysis of variance indicated a significant effect of successional stage on average species richness ($F_{3,8} = 13.91$, $p = 0.002$; Fig. 3a). Species richness increased monotonically along the successional gradient (ANOVA, linear trend: $F_{1,8} = 40.41$, $p < 0.001$) and old-growth forest plots (mean species richness per 1 m^2 plot: 12.7, range: 12.0 – 13.4) had more than twice as many species as did plots of the youngest successional stage (mean species richness: 4.9, range: 3.7 – 7.0). Contrary to our expectations and despite the marked differences in species richness among successional stages, we found only a small effect on metrics of the niche space occupied by ant communities (Fig. 3b and c). SES values for the CHA ranged from 0.57 to 0.37 and SES values for mNND ranged from -0.78 to 0.55 per site (occurrence weighted null model). Assuming a normal distributions of deviations, ca. 95% of the SES values should fall between -2.0 and 2.0. Therefore, species communities in all sites appeared to be random subsets of the overall species pool. Results for the equiprobable null model are qualitatively similar. An analysis of variance indicated no statistically significant effect of successional stage on CHA values ($F_{3,8} = 3.40$, $p = 0.07$) but for SES values for mNND ($F_{3,8} = 5.94$, $p = 0.02$). However, this effect was mainly due to the large variation in SES values for mNND among sites of the youngest successional stage and was no longer significant when these sites were excluded from the analysis ($F_{2,6} = 2.42$, $p = 0.17$).

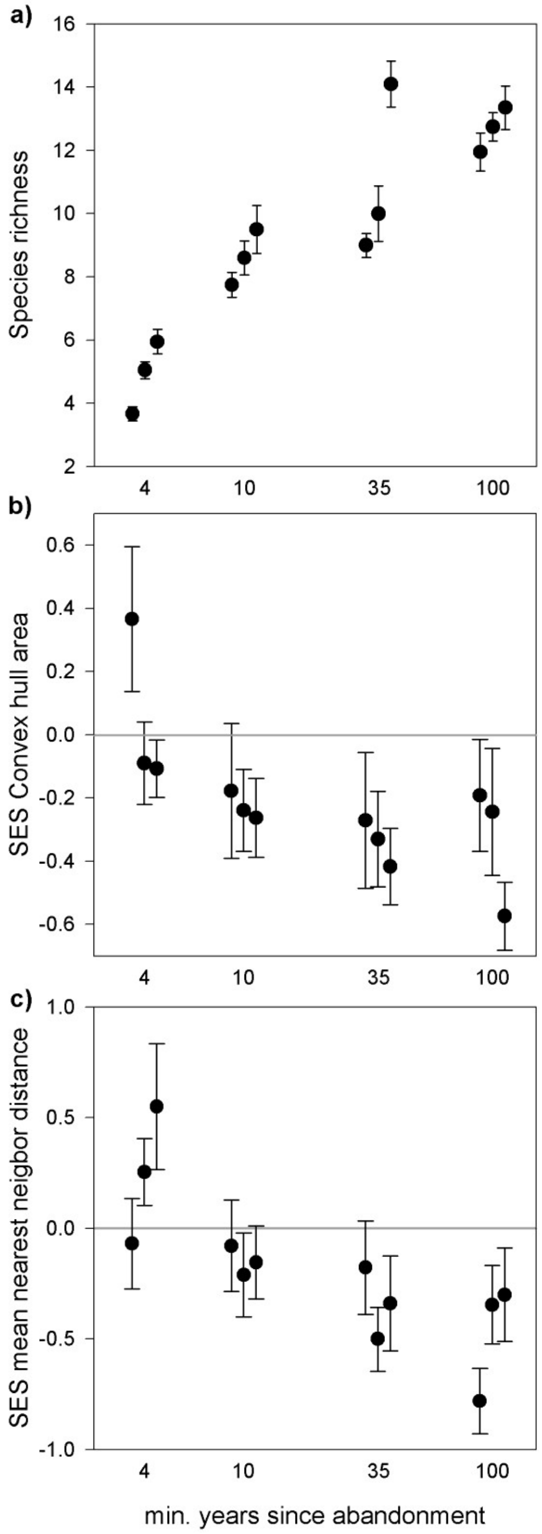


Figure 3: The relationship between minimum age of forest (log10 of years) and (a) species richness, (b) SES for convex hull area and (c) SES for the mean nearest neighbor distance. In each case the circles represent mean of values (± SE) for each site (12 sites).

Discussion

We identified patterns of community assembly in leaf litter ants from an analysis of functional traits and compared these with expectations from two null models. We examined changes in niche space occupation of ant communities in relation to species richness and along a successional gradient of tropical forests. Results are consistent among the two null models used. Rare species tend to occupy more peripheral positions in niche space relative to common species (Fig. 1, inlet). Therefore, the occurrence-weighted null model appears to be the more appropriate null model. We were able to draw two main conclusions from our analysis.

First, our results support the idea that assembly rules based on species interactions such as limiting similarity (MacArthur and Levins 1967) or competitive exclusion (Hardin 1960) are not important for leaf litter ants in a tropical forest. Coexisting species were generally more similar, as measured by the mean nearest neighbor distance in niche space, than expected under the null model of randomly assorted species. Furthermore, the comparison of observed communities with communities expected under the null models revealed that although the invasion of species into local communities significantly increased the occupied niche space, most species were included in the functional space already occupied by resident species. These results are consistent with the species packing mechanism proposed by Ricklefs and Miles (1994).

Second, we found no evidence for changes in the pattern of community assembly along the successional gradient. Species richness increased significantly from early to late successional stages and in an earlier paper we demonstrated that on the taxonomic level of genera the composition of communities along the successional gradient is nested (Bihn et al. 2008a). Despite these marked differences in the diversity and composition of ant communities, the functional traits of coexisting species were similar to expectations from the null models. We found a weak trend for species packing to increase and the total niche space occupied to decrease with successional age. This pattern is opposite to the expectations from the model of Weiher and Keddy (1995).

The apparently non-interactive assembly of ant communities in our study was a rather surprising result and contrasts with many studies which suggest that competitive interactions structure ant communities (Levings and Traniello 1981; Savolainen and Vepsäläinen 1988; Morrison 1996; Hölldobler and Wilson 1990). Since the seminal paper of Hutchinson (1959) many studies have based their search for competition in natural communities on one functional trait alone, namely body size. Several studies on patterns of body size distribution in ant communities have shown that under certain circumstances (relating to spatial scale and habitat) uniform distributions of body sizes among coexisting species exist, which indicates that competitive interaction might structure these communities (Gotelli and Ellison 2002; King 2007; Sanders et al. 2007). Evidence for the importance of interspecific competition in structuring ant communities was also found in an ecomorphological study on *Rhytidiponera* assemblages in Australia (Nipperess and Beattie 2004). These studies demonstrate that for some ant communities the distribution of ecological traits among coexisting species is concordant with the hypothesis that interspecific competition influences ant community structure.

A closer look on the literature demonstrating competitive interactions among ants reveals a predominance of studies conducted on relative species-poor communities in the temperate and arid regions. Furthermore, evidence for competitive interactions in ground foraging ant communities, as opposed to those in the canopy, is sparse. For example, one line of evidence for competitive interactions among coexisting ant species argues that one should find a regular distribution of ant colonies, if colonies deplete resources and kill foundress queens near established nests (Levings and Traniello 1981). In a summary of the evidence, Levings and Traniello (1981) suggest that this is often the case. Among the many studies on the spatial distribution of ant colonies, only two studies consider tropical leaf litter ant communities and these two studies report contradictory results (Levings and Franks 1982; Soares and Schoereder 2001). Other studies demonstrate behavioral interference competition within and between ant species that use similar resources (Perfecto 1994; Cole 1983; Andersen et al. 1991). While these studies clearly show that dominant species can restrict the access of subordinate species to local resources, there is little evidence that this leads to the complete exclusion of species from local communities (Gibb and Hochuli 2004). As pointed out by Andersen (2008), ant colonies are extremely persistent once established. The social and modular organization of ant colonies effectively buffers against adverse biotic or abiotic conditions and might prevent the complete local exclusion of subordinate species by behaviorally dominant species. Overall the evidence for competition to be a major structuring force on ground foraging ant communities in tropical forests is weak and our study is a further example.

Why are the effects of competition not reflected in the occupancy of niche space in tropical leaf litter ants in the Atlantic Forest of Brazil? Two phenomena might preclude the influence of interspecific competition on tropical leaf litter ants. First, the low influence of interspecific competition on community structure might be a result of the spatially heterogeneous environment. In homogeneous environments, stable coexistence is only possible when different species specialize on different resource types (Hardin 1960; MacArthur and Levins 1967) but this may not be necessary in spatially heterogeneous environments. Tropical leaf litter ants are generally small in body and colony size. For organisms of this size the microhabitat of the leaf litter represents a complex three dimensional habitat (Kaspari and Weiser 1999; Irschick and Garland Jr. 2001) which hinders movement and inhibits the defense of resources in a large area from potential competitors. Additionally, many ant species are opportunistic scavengers which feed on a variety of food items like dead insects, fruit fragments, seeds and many others (Carrol and Janzen 1973). The availability of these food items in the leaf litter are highly unpredictable in space and time which make them difficult to monopolize and exclude other species from this resource. Thus, the spatial heterogeneity of the leaf litter habitat might facilitate the coexistence without specialization on different resource types. Second, army ants (Ecitoninae) are ubiquitous and important predators on social insects and other arthropods in Neotropical forests (Franks 1982; Otis et al. 1986). Raids of army ants limit the population density of dominant ants in the leaf litter, yet seldom kill entire colonies. Thus, other ants can take advantage of their low density in recently raided areas. Similarly, dominant ant species tend to be more vulnerable to parasitoids which might limit their influence on other species in the local assemblage (Feener, Jr. 2000; LeBrun and Feener 2002). Together, these macro- and micropredators might limit the influence of behaviorally dominant species on subordinate species in communities of tropical leaf litter ants. Therefore, one might conclude that newly arriving queens might be very likely to find competition free space in the leaf litter and that the suitability of local resources (e.g. nest sites, food) and habitat conditions (e.g. temperature, humidity) are the most important factors for the success of the establishment of new colonies, and ultimately influences the structure of ant communities on local scales.

The observed pattern of species richness and the distribution of communities in niche space of communities along the successional gradient agree with the above arguments. While species richness increased significantly from early to late successional stages, patterns of ant communities in niche space are relatively similar along the gradient. The increase in species richness was mainly driven by the long tail of rare species, i.e. the proportion of rare species in communities was larger in late than in early successional stages (note that communities were nested along the gradient (Bihn et al. 2008a)). Rare species tended to have more peripheral position in niche space (Fig. 1, inlet). This indicates that these species occupied rather unique niches. While some part of the increase in species richness along the successional gradient might therefore be explained by the unique niches of some rare species, this alone cannot explain the overall increase in species richness. If the increase in species richness was exclusively accomplished by the recruitment of species with unique and unoccupied niches, we should have found a significant increase in total niche space, but the occupied niche space was relatively invariant along the gradient. The niche space of observed ant communities was generally lower than expected from randomly assorted communities This suggests that an environmental filter is acting on local ant communities and only ant species for which local resources and conditions are met, may successfully colonize a given patch. This is concordant with the results reached by Soares et al. (2001) who concluded that species saturation of leaf litter ant communities in South-East Brazil is produced by habitat specialization and/or by stochastic equilibrium and not by interactive processes. Leaf litter ants are known to react sensitively to variations in the microclimate of the leaf litter (Whitford and Ettershank 1975; Kaspari 1993). Daily variations in the temperature of the leaf litter were more pronounced in early successional stages than in late successional stages (unpublished results). These extremes in the microclimate of early successional stages might exclude many ant species which are adapted to a narrow range of temperature and humidity typical of old-growth forests. Leaf litter ants, like other soil and litter invertebrates, depend on the quantity and quality of the dead organic matter in their habitat. Nest availability, food abundance and microclimatic stability are all likely mediated by the depth of the leaf litter. The volume of the leaf litter increases along the successional gradient and ant species richness is significantly and positively correlated (Fig. 4). The diversity of trees also increases from early to late successional stages of secondary forests (K. Martins & S. Meyer, personal communication) and this inevitably leads to a similar pattern in the diversity of the leaf litter. The accompanying changes in the stoichiometry of the leaf litter have been shown to affect the structure of the litter fauna (Bihn et al. 2008b; McGlynn et al. 2007). Armbrecht et al. (2004) demonstrated experimentally that the diversity of nesting resources (twigs from different tree species) affects the diversity of twig-nesting ants in the leaf litter of a coffee agroecosystem in Colombia. Because the involved ant species appear to have no specialization on particular tree species, resource partitioning is no plausible explanation for the observed phenomenon. This exemplifies how the diversity of the litter might affect the diversity of leaf litter ants without the involvement of competitive interactions.

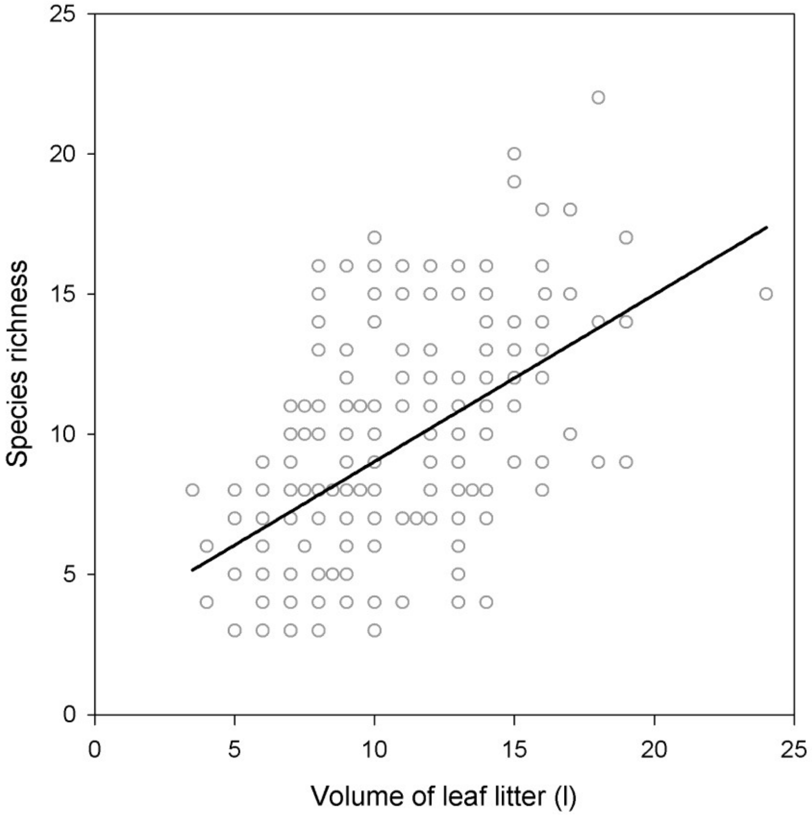


Figure 4: The relationship between volume of leaf litter and ant species richness for 230 plots (1m²). Species richness is positively correlated with volume of leaf litter ($r = 0.52$, $p < 0.001$).

Our study adds to the growing evidence that resource availability and habitat conditions, rather than competition, are the major force structuring communities of tropical leaf litter ants (Byrne 1994; Kaspari 1996a; Kaspari 1996b; Soares and Schoereder 2001; Theunis et al. 2005). If this is true, local species richness is primarily a product of the suitability of the local environment for species adapted to it. The differences in this suitability for leaf litter ants might be the major factor for the increase in species richness along the gradient of secondary tropical forests under study. The number of species in each successional stage is then limited by the number of species in the regional species pool adapted to the local environment.

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5

Ecological stoichiometry along a gradient of forest succession: Bait preferences of litter ants

with Manfred Verhaagh and Roland Brandl

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Abstract

We examined bait preferences of litter ants along a successional gradient of forests in the Atlantic Forest of Brazil. The ants preferred protein-based baits in secondary forests, yet preferred carbohydrate-based baits in old-growth forests. This suggests a shift in stoichiometric balances between secondary and old-growth forest which might have an impact on the functional interactions in these ecosystems. Therefore, the ecological services offered by secondary habitats may be quite different from those offered by old-growth forests.

Introduction

The theory of ecological stoichiometry assumes that consumers maintain elemental homeostasis in body composition within limited bounds (Sterner and Elser 2002). Therefore, when confronted with alternative food choices, organisms will prefer nutrients that are relatively rare. The ratios of available nutrients in ecosystems can drive both the growth rate of individual organisms and the abundance of organisms within a species at the population level (Rosemond et al. 2001), and ultimately the organization of species communities (Tilman 1982). Thus, resource ratios have an important impact on ecological and evolutionary processes. For example, most of the primary production in tropical forests is not consumed by herbivores, but is returned to the environment as detritus, which fuels the detritus-based food web (Moore et al. 2004). The variation of nutrient signatures among the leaves, fruits and seeds that fall from the canopy produces a mosaic of resources on the forest floor. The composition, quality (especially the carbon-nitrogen ratio, C/N), and total biomass of the detritus may shape the structure and dynamics of communities in the detritus-based food web

Ants (Hymenoptera: Formicidae) are useful taxa for the study of nutrient ratios in tropical forests. The majority of tropical litter ants are opportunistic foragers, taking a combination of plant exudates, seeds, and dead or living animal matter (Levings 1983; Tobin 1995). The preference of foragers for particular food items depends on the availability of items elsewhere in the environment (Kay 2002; 2004). If the forager determines that the item in question is a scarce resource, it may then communicate information about the food item to its nestmates and recruit additional foragers. The differential ant activity in response to encountering different types of food may therefore unveil underlying stoichiometric balances and ecological processes.

We analyzed leaf-litter foraging ants from different successional stages of secondary forests in their preference for baits that contained carbohydrate or protein resources in comparison to those from old-growth forests. We assumed that ant workers prefer the scarce resource when confronted with both. We expected that if there were differences in the stoichiometric balances provided by secondary and old-growth forests, there would be a shift in the preferences of ants that inhabit secondary and old-growth forests.

Methods

In December 2006, we conducted bait-choice experiments (Kaspari and Yanoviak 2001; Hahn and Wheeler 2002) in secondary and old-growth forests in the Atlantic Forest of SE Brazil in the Rio Cachoeira Nature Reserve (25°18'51" S, 48°41'45" W; coastal region of the Brazilian state of Paraná). Lowland and submontane forests originally covered the area, but these dense ombrophilous forests have suffered intense exploitation and large parts of them have been converted to pasture. The resulting landscape consists of old-growth forests and secondary forests in various stages of succession. We ran bait-choice experiments in three successional stages of secondary forests (~8 yr, 13–18 yr, 28–53 yr) and in old-growth forests (> 100 yr). For each successional stage, we established three replicated sites (20 × 50 m; for further details on study region and design, see Bihn et al. 2008). We installed eight bait stations in the leaf litter of every study site, each consisting of two bait types: tuna (hereafter N baits) and honey (hereafter CHO baits), which gave a total of 192 baits, 96 bait stations, and 12 study sites. Bait stations were separated by a minimum distance of 10 m. The size of the baits was consistent (~2 cm in diameter), and the baits were placed on round filter papers 20 cm apart. We recorded the number of ants that visited each bait at 2, 14, 26, 38 and 50 min after placement. Voucher specimens of ants were collected at the end of the observation period. All observations were made between 1000 h and 1600 h in dry weather conditions.

Results

Ants encountered the baits rapidly and recruited nest-mates (Fig. 1). We observed ants at 89 of the 96 bait stations and recorded a total of 44 species. The most common ants observed at the baits were species of *Pheidole*, *Solenopsis* and *Crematogaster*. 34 species were recorded at CHO baits and 37 species at N baits. The overlap of the species that visited the two bait types was 61 percent. The number of species per site did not differ among successional stages (range = 5–14, mean = 8.3 ± 0.77 SE; ANOVA: P = 0.67). The number of attracted species per site also did not differ between CHO and N baits (mean = 5.4 ± 0.51 and 6.2 ± 0.67, respectively; P = 0.41).

In all successional forest stages, the abundance of ants at CHO and N baits increased monotonically with time (Fig. 1). We analyzed ant activity at baits (*i.e.*, abundance after 50 mins) with a four-factor partly-nested ANOVA. Factors were: successional stage (four levels, fixed); sites nested within successional stage (three levels, random); bait stations nested within sites of each successional stage (eight levels, random) and bait type (two levels, fixed). Ant abundance data were square-root transformed to approximate assumptions of normality. Neither successional stage ($F_{3,8}$ = 0.19, P = 0.90) nor bait type ($F_{1,8}$ = 1.06, P = 0.33) had a significant effect on ant abundance. The preference of the ants for the type of bait changed along the successional gradient (successional stage × bait type: $F_{3,8}$ = 5.52, P = 0.02). In young successional stages, N baits attracted more ants than CHO baits, whereas in late successional stages, CHO baits attracted more ants (Fig. 1).

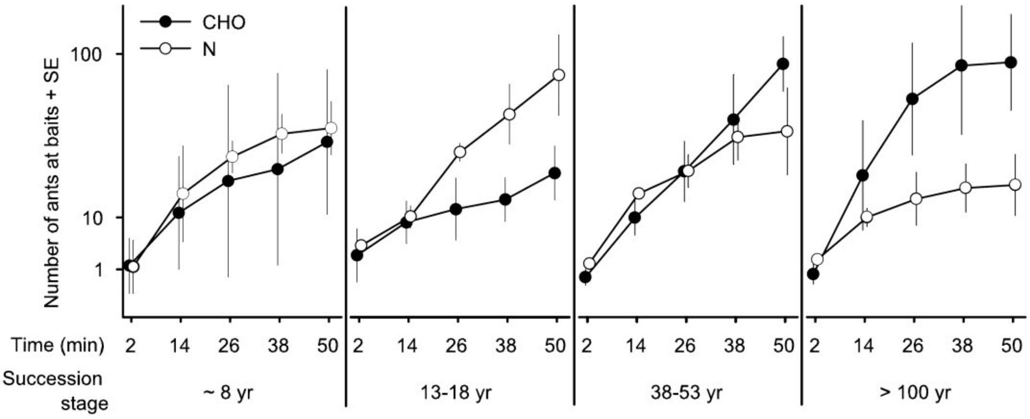

Figure 1. Results of bait-choice experiments in three successional stages of secondary forest and old-growth forest (> 100 yr) in the Atlantic Forest of Brazil. The mean number of ants (square root transformed sum of ants at all bait station per site) at different bait types (honey or tuna baits) after 2, 14, 26, 38 and 50 min is shown; N = 3 for each mean.

One explanation for the pattern of observed bait preference may be differences in community composition of ant species, with particular species that prefer N baits occurring in young forests and different species that prefer CHO baits occurring in old forests. We tested this possibility by repeating our analysis, but including only species that were common to young (stages: ~8 yr and 13–18 yr) as well as old (stages: 28–53 yr and old-growth forests) successional stages (12 species). We pooled ant abundance after 50 mins for each bait type and site for this analysis. Again, we found a shift in bait preference along the successional gradient ($F_{3,8}$ = 4.09, P = 0.049). In all successional stages of secondary forests, the activity of ants at N baits was higher than at CHO baits, but in old-growth forests, the ants preferred CHO baits to N baits. This suggests that the difference in bait preference along the successional gradient is not exclusively a result of different species with different food preferences occurring in young and old forests, but is, rather, the result of the ants changing their food preference in response to the type of forest and the distribution of nutrients contained therein.

Discussion

What might explain this shift in bait preference? The structure of detritus-based food webs is correlated with the availability and quality of dead organic matter (Wardle 2002). The volume of leaf litter increased along the studied gradient (J. H. Bihn, unpub. data) and other studies in tropical forests have shown repeatedly that the nitrogen concentration of leaf litter increases during secondary succession (Xuluc-Tolosa et al. 2003; Vasconcelos and Laurence 2005). In addition, the abundance of other groups of macroarthropods, which are an important source of nitrogen for ants, increases along the successional gradient under study (P. Hopp, pers. comm.). A higher availability of nitrogen in old successional stages might have contributed to the observed shift in bait preferences.

Alternatively, carbohydrates could be more available to ants in young successional forests than in old successional stages. Extrafloral nectaries and honeydew (excretions from herbivorous insects) are two important carbohydrate sources for animals in tropical forests and most frequently visited by ants. Such CHO-rich resources are more commonly consumed by arboreal species, but ground-nesting ants frequently climb onto plants to search for this type of food (Oliveira and Brandão 1991). Percentage occurrence and cover of plants with extrafloral nectaries is higher in secondary habitats than in old-growth forests in tropical areas (Schupp and Feener 1991; Fiala and Linsenmair 1995). This could result in a higher availability of carbohydrates for ants in secondary forests of early succession.

We have shown that tropical litter ant assemblages prefer N baits in young successional stages of secondary forests, yet prefer CHO baits in late successional stages of secondary forests and in old-growth forests. This change in preference may be due to the higher availability of nitrogen in late successional stages of secondary forests and/or the higher availability of carbohydrates in young successional stages. While we can only speculate on the causes of the observed pattern, our results clearly suggest a shift in stoichiometric balances between secondary and old-growth forest which might have an impact on the functional interactions in these ecosystems. For example, ants are considered to be key predators in tropical forests (Hölldobler and Wilson 1990) and are likely to influence the composition and density of detrivores. The change in preferences of CHO vs. N might modulate the predation pressure exerted by ants on other invertebrates in the leaf litter. Because soil invertebrates have a considerable effect on litter decomposition rates (Hättenschwiler et al. 2005) this may ultimately effect nutrient (re)cycling in the ecosystem. Therefore, the ecological services (e.g. nutrient cycling) offered by secondary habitats may be quite different from those offered by old-growth forests. If our results are typical for tropical forests it is doubtful that all types of forest cover (e.g. old-growth forests, secondary forests and exotic tree plantations) offer similar ecosystem services and habitat for forest-adapted species as recently suggested (Wright and Muller-Landau 2006). Further studies are needed to bridge this gap in our understanding of the value of secondary forests for conservation in the tropics and to build a sound empirical base for policy recommendations.

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6 Summary

Tropical forests are the most diverse of all terrestrial ecosystems. Though occupying only 7% of the Earth‘s land surface, they probably sustain over two-thirds of all species. Tropical forests are disappearing at fast rates and this has been identified as a major threat to global biodiversity. Deforestation, however, is rarely permanent — converted land is exhausted, abandoned and allowed to regrow. Critical for the future of biodiversity is the degree to which these secondary forests can replace old-growth forests as habitat for forest dwelling species and fulfill similar ecosystem functions. Yet, relatively little is known about the value of secondary forests for the conservation of biodiversity and ecosystem functions.

The main objective of my dissertation was to evaluate to what degree tropical secondary forests contribute to the conservation of biodiversity and ecosystem functions. To do so, I used soil and leaf-litter ants (Hymenoptera: Formicidae) — a dominant, species rich, and functionally important group of invertebrates — as model organisms. My approach was twofold: On the one hand, I analyzed the effects of secondary forest succession on various facets of the diversity and community structure of ants (chapter 2 & 3). On the other hand, I investigated the successional changes in the ecosystem and how these influence the community assembly of ants (chapters 4 & 5). All studies were carried out in the Rio Cachoeira Nature Reserve in the Atlantic Forest of Brazil. I sampled the ant community in a total of 27 study sites that encompassed a gradient of naturally regenerating forests in three different successional age stages (~5 years, 10-15 years & 35-50 years after abandonment of pastures). Additionally, I also sampled the ant community in pastures and old-growth forests for comparison.

Richness and composition of ant assemblages in secondary forests recovered slowly and did not approach conditions typical of old-growth forests. The distribution of ant taxa along the successional gradient was arranged in a nested pattern — ant taxa of younger successional stages were a subset of taxa present in older stages. Edaphic conditions had only minor influence on the recovery process. Overall, richness of ants was lower at study sites with water-logged soils than at sites where soils did not exhibit hydromorphic properties. The hypogeic ant assemblage recovered more slowly than the epigeic assemblage. Moreover, estimated recovery times of 50 to several hundred years suggest, it would take much longer than previously presumed for complete recolonization.

The functional diversity of ant communities was assessed using a set of important functional traits. It became evident that species diversity is closely linked to the functional diversity of ant communities. Since functional complementarity among coexisting species was high, reduced species diversity in secondary forests resulted in proportionally reduced functional diversity of local ant communities. Rare, but functionally unique species, were largely missing in secondary forests. These results suggest that secondary forests may only provide reduced levels of ecosystem functions in comparison to old-growth forests.

Knowledge about the rules that govern the assembly of local communities from the regional species pool is useful in providing a scientific foundation for the conservation of biodiversity. Favorable resource availability and habitat conditions appeared to be more important for the assembly of ant communties from the regional species pool than interactive processes such as competition among species. Despite marked differences in species richness and composition of ant communities, the pattern of community assembly varied little in forests of different successional stages. In a field experiment, I studied the resource availability for leaf-litter ants in more detail. I examined bait preferences of ants (protein baits vs. carbohydrate baits) in secondary forests and old-growth forests. The ants preferred protein baits in secondary forests, yet preferred carbohydrate baits in old-growth forests. This suggests a shift in stoichiometric balances between secondary and old-growth forests, which might impact the functional interactions in these ecosystems.

In conclusion, secondary forests do not act as refuges for many species which currently occur in discontinuous patches of old-growth forest in the highly endangered Atlantic Forest of Brazil. The structure of ant communities seems to be primarily a product of local environmental conditions, such as the stoichiometric balances of the ecosystem. These environmental conditions are much altered in secondary forests in comparison to old-growth forests and not many forest species can cope with these conditions. The observed loss of both species and functional diversity in secondary forests offers no reason to believe that the ecological functions provided by secondary forests are buffered against species loss through functional redundancy. Therefore, secondary forests might provide only reduced levels of ecosystem services. These results highlight the crucial importance of old-growth forests for the conservation of ecosystem functions and biodiversity in the tropical wooded landscape.

7 Zusammenfassung

Tropische Regenwälder sind die artenreichsten aller terrestrischen Ökosysteme. Obwohl sie nur etwa 7% der Erdoberfläche bedecken, beherbergen sie mehr als zwei Drittel aller Arten. Die rasch fortschreitende Zerstörung dieser Wälder stellt eine grosse Bedrohung für die biologische Vielfalt der Erde dar. Jedoch ist die Zerstörung des Waldes selten von Dauer — die landwirtschaftlichen Erträge der umgewandelten Flächen lassen nach, die Nutzung wird aufgegeben und die natürliche Waldregeneration setzt ein. Entscheidend für die Zukunft der Biodiversität in tropischen Wäldern ist, in wie weit diese Sekundärwälder als Ersatzhabitate für Waldarten fungieren und ähnliche Ökosystemfunktionen wie Primärwälder ausüben können. Das Wissen über den Wert von Sekundärwäldern für den Schutz von Biodiversität und Ökosystemfunktionen tropischer Wälder ist jedoch bislang unzureichend.

Ziel der vorliegenden Arbeit ist es, einen Beitrag zur Beurteilung tropischer Sekundärwälder für den Schutz von Biodiversität und Ökosystemfunktionen zu leisten. In meiner Arbeit nutzte ich Ameisen (Hymenoptera: Formicidae) — eine dominante, artenreiche und funktionell wichtige Invertebratengruppe — als Modelorganismen. Ich analysierte einerseits den Effekt von sekundärer Waldsukzession auf verschiedene Aspekte der Diversität und Struktur von Ameisengemeinschaften (Kapitel 2 & 3). Andererseits untersuchte ich die Veränderungen im Ökosystem und wie diese die Zusammensetzung der Ameisengemeinschaften beeinflussen (Kapitel 4 & 5). Alle Untersuchungen wurden im Naturreservat Rio Cachoeira im Küstenregenwald Brasiliens (Mata Atlântica) durchgeführt. Ich besammelte die Ameisengemeinschaft auf insgesamt 27 Untersuchungesflächen, die einen Gradienten der natürlichen Waldsukzession (3 Altersstadien: ~5, 10-15 & 35-50 Jahre) umfassten. Zusätzlich beprobte ich zum Vergleich die Ameisenfauna von Weiden und Primärwäldern.

Nach der Aufgabe der landwirtschaftlichen Nutzung erholte sich die Diversität der Ameisen in Sekundärwäldern in Bezug auf Artenreichtum und Zusammensetzung der Gemeinschaften nur langsam. Artenreichtum und Zusammensetzung der Ameisengemeinschaften erreichten selbst in den ältesten untersuchten Sekundärwäldern nicht die Verhältnisse wie sie für Primärwälder typisch sind. Die Verteilung der Ameisentaxa entlang des Sukzessionsgradienten folgte einem verschachtelten Muster: Taxa in jüngeren Sukzessionsstadien waren eine Teilmenge der Taxa, welche auch in älteren Sukzessionsstadien lebten. Die

Bodenbedingungen hatten nur einen geringen Einfluss auf das generelle Muster der Regeneration der Ameisengemeinschaft. Allgemein war der Artenreichtum in Wäldern mit vernässten Böden geringer als in Wäldern mit Böden ohne hydromorphe Merkmale. Die hypogäische Ameisengemeinschaft regenerierte langsamer als die epigäische Ameisengemeinschaft. Darüber hinaus weisen Schätzungen von 50 bis zu mehrere hundert Jahre für eine vollständige Regeneration, auf einen wesentlich längeren Zeitraum hin als bisher angenommen wurde.

Die funtionelle Diversität der Ameisengemeinschaft war eng gekoppelt an ihre Arten-Diversität. Da Artengemeinschaften von Ameisen eine relativ geringe funktionelle Redundanz aufwiesen, resultierte die verrringerte Arten-Diversität in Sekundärwäldern in eine proportional verringerte funktionelle Diversität der Ameisengemeinschaften. Seltene, jedoch zugleich funktionell einzigartige Arten, fehlten in der Regel in Sekundärwäldern. Diese Ergebnisse weisen darauf hin, daß Sekundärwälder im Vergleich zu Primärwäldern lediglich eine reduziert Ökosystemfunktion ausüben können.

Das Wissen über die Mechanismen nach denen sich lokale Artengemeinschaften aus dem regionalen Artenpool zusammensetzen, ist eine wertvolle wissenschaftliche Basis für den Schutz von Biodiversität. Günstige Resourcenverfügbarkeit und Habitatbedingungen übten einen stärkeren Einfluss auf die Zusammensetzung der Ameisengemeinschaften aus als interaktive Prozesse, wie etwa Konkurrenz zwischen den Arten. Trotz ausgeprägter Unterschiede in Artenreichtum und Zusammensetzung lokaler Ameisengemeinschaften, variierte das Muster der Besetzung des Nischen-Raums entlang des Sukzessionsgradienten nur wenig. Dies weist darauf hin, daß sich die Mechanismen, nach denen sich lokale Artengemeinschaften aus dem regionalen Artenpool zusammensetzen, entlang des Sukzessionsgradienten nicht wesentlich ändern. In einem Feld-Experiment untersuchte ich eingehender die Variabilität der Resourcenverfügbarkeit für Ameisen. Ich prüfte die Köderpräferenzen von Ameisen (Protein- im Vergleich zu Kohlenhydrat-Ködern) in Sekundärwäldern und Primärwäldern. In Sekundärwäldern präferierten Ameisen Protein-Köder, während sie in Primärwäldern Kohlenhydrat-Köder bevorzugten. Dies weist auf eine Verschiebung der stoichiometrischen Gleichgwichte zwischen Sekundär- und Primärwäldern hin, was die funktionellen Interaktionen in diesen Habitaten beeinflussen könnte.

Zusammenfassend lässt sich feststellen, daß Sekundärwälder nur für einen relativ geringen Teil typischer Waldarten als Ersatzhabitate fungieren können. Die Verbreitung vieler Arten ist gegenwärtig auf Primärwald-Fragmente des stark bedrohten Atlantischen Küstenregenwalds Brasiliens beschränkt. Die Struktur lokaler Ameisengemeinschaften ist in erster Linie ein Produkt der lokalen Umweltbedingungen. Diese Umweltbedingungen, welche auch die stoichiometrischen Gleichgewichte des Ökosystems einschliessen, sind in Sekundärwäldern im Vergleich zu Primärwäldern stark verändert. Viele Waldarten kommen mit diesen veränderten Umweltbedingungen nicht zurecht. Der gleichzeitige Verlust von Artendiversität und funktioneller Diversität in Sekundärwäldern gibt keinen Anlass zur Hoffnung, daß die Auswirkungen des Artenverlustes in Sekundärwäldern durch funktionelle Redundanz der Ameisengemeinschaften abgemildert werden könnte. Folglich können Sekundärwälder nur einen reduzierten Teil der ökosystemaren Dienste von Primärwäldern bereitstellen. Diese Ergebnisse unterstreichen daher die kritische Bedeutung von Primärwäldern für den Schutz von Biodiversität und Ökosystemfunktionen in der tropischen Waldlandschaft.

8 Appendix

Supporting Material

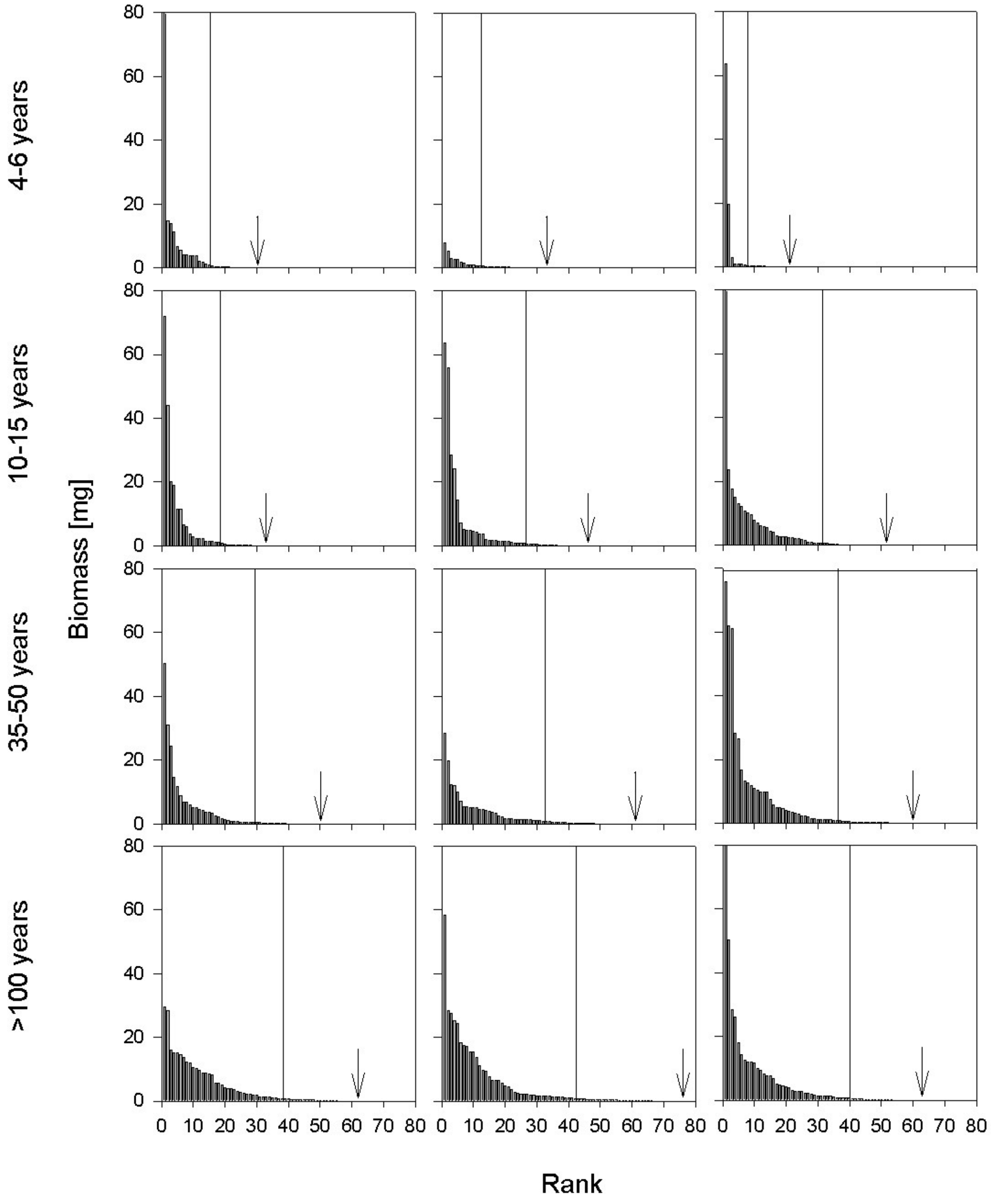

Figure A. Rank-biomass diagrams for ants in each of the 12 study sites. Diagrams are grouped by successional stage (n = 3 sites for each successional stage) and ordered from top to bottom by years since abandonment. All at the same scale. All species right of the vertical line had a biomass of less than 0.5 mg and were excluded from the analysis (see methods). Arrows indicate the species with the lowest biomass in each site.

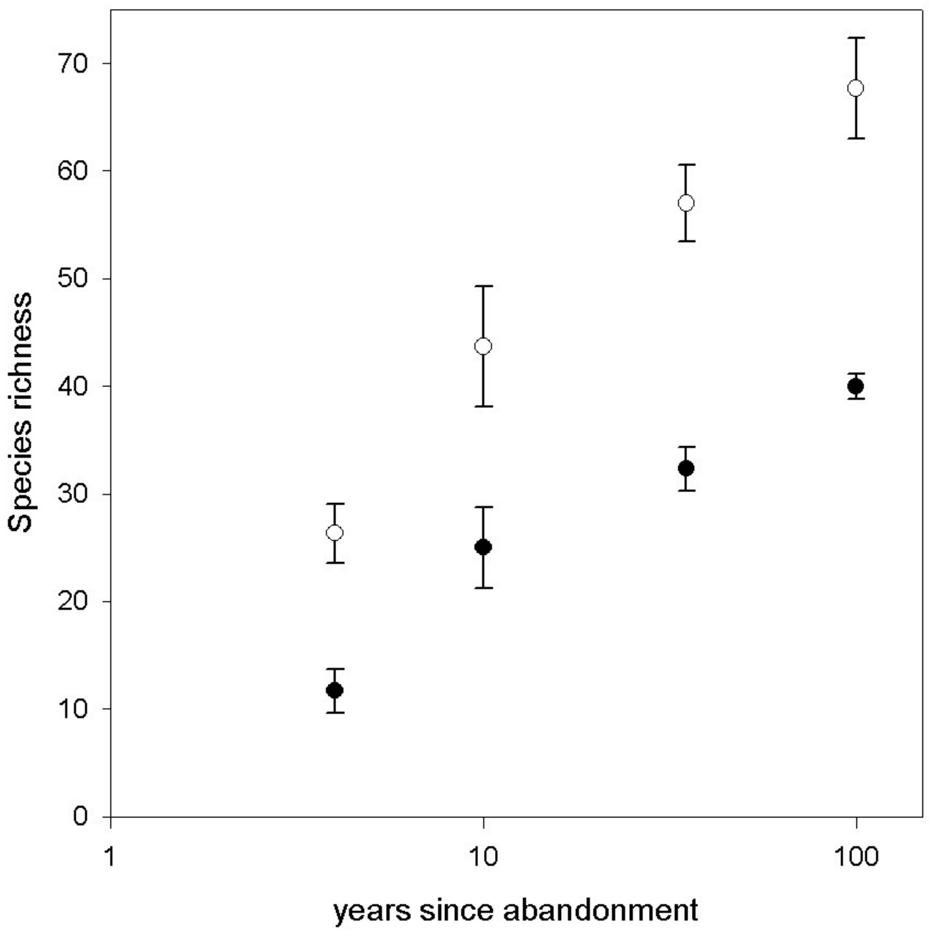

Figure B. Species richness for each successional stage (mean ±SE; n = 3 for each stage) before (open circles) and after (shaded circles) filtering of species lists (see methods).

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Abgrenzung der Eigenleistung

Soweit nicht anders erwähnt, wurden alle Studien von mir selbst geplant und durchgeführt, sowie anschließend in Form eines Manuskriptes ausgewertet. Das abschließende Verfassen der Manuskripte erfolgte in Zusammenarbeit mit meinem Betreuer Prof. Dr. Roland Brandl.

Die Analysen der stabilen Isotope (Kapitel 3 & 4) wurden von Prof. Dr. Gerhard Gebauer im Labor für Isotopen-Biogeochemie der Universität Bayreuth durchgeführt.

Die Feldarbeiten zur Studie in Kapitel 6 wurde in Zusammenarbeit mit Dr. Manfred Verhaagh (Staatliches Museum für Naturkunde Karlsruhe) durchgeführt. Er kommentierte außerdem die Manuskripte in Kapitel 2 und 6.

Dr. Martin Brändle kommentierte das Manuskript in Kapitel 2.