Recovery of litter inhabiting beetle assemblages during forest regeneration in the Atlantic forest of Southern Brazil

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Abstract. 1. As mature tropical forests disappear, secondary forests with their potential to conserve mature tropical forest species are increasingly of interest in a conservation context.

2. We investigated the recovery of litter inhabiting beetle diversity and composition during natural forest regeneration in the coastal submontane forest of Southern Brazil, using chronosequences on two different soil types: cambisol and gleysol. Secondary forests, ranging in ages from 5 to 50 years, as well as old-growth forests were studied. Beetles were sifted from leaf litter and extracted using the Winkler technique.

3. Young secondary forests had a very low species density and a significantly different and heterogeneous species composition compared to old-growth forests. During forest regeneration, species density greatly increased and the species composition of older secondary forests was similar to that of old-growth forests. The recovery pattern of species density and composition differed between soil types; nonetheless, they showed the same tendencies generally. Thus, mature secondary forests of about 35–50 years can be assumed to contribute substantially to the maintenance of forest beetle species.

4. Litter quantity was not only significantly correlated with species density; but, even reflected the density pattern of both soil types. Thus, litter quantity is an important factor for maintaining or recovering high beetle densities. The composition of beetle assemblages was strongly affected by soil type. Thus, soil type should be considered in regional biodiversity monitoring and conservation actions.

Key words. Biodiversity, Coleoptera, forest regeneration, insect conservation, Mata Atlântica, old-growth forest, secondary forest, soil type, species density, species richness

Introduction

A major threat to global biodiversity is the ongoing destruction of mature tropical forests (Dirzo & Raven, 2003). Although

future deforestation rates and their consequence for species extinction is scientifically debated (Brook *et al.*, 2006; Wright & Muller-Landau, 2006a,b; Gardner *et al.*, 2007b; Laurance, 2007), it is widely agreed that the proportion of secondary forests to total forest area will further increase (Perz & Skole, 2003; Aide & Grau, 2004; FAO 2009). This trend makes it important to evaluate the potential of secondary forests to act as refuges for forest species (Lawton *et al.*, 1998; Wright, 2005). However, data on the recovery of faunal assemblages during forest

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regrowth are still sparse and mostly confined to a few popular groups, such as birds and ants (e.g. Dunn, 2004; Sodhi *et al.*, 2005; Silva *et al.*, 2007; Bihn *et al.*, 2008; but, see Basset *et al.*, 2008). Prediction of changes in species richness, among faunal groups using indicator taxa, often fails (Prendergast, 1997; Lawton *et al.*, 1998; Wolters *et al.*, 2006; Barlow *et al.*, 2007a; Basset *et al.*, 2008); therefore, it is crucial to increase the database of faunal inventories and their response patterns (Schulze *et al.*, 2004). This is especially true for tropical insect communities of highly specific microhabitats, such as leaf litter (Lewinsohn *et al.*, 2005).

Beetles affect many important ecosystem processes in forests including litter decomposition, nutrient flow and food web regulation. They modulate their environment at different trophic levels being predators as well as decomposers. In tropical forests, beetles are particularly species rich and abundant (Hammond, 1990; Nadkarni & Longino, 1990; Didham *et al.*, 1998; Stork & Grimbacher, 2006) and reflect the richness of insect communities (Moeed & Meads, 1985). However, litter inhabiting beetles of tropical forests have rarely been studied owing to their diminutive size and poor taxonomical description. Most available studies that examined the effect of habitat loss and modification on ground related beetles in neotropical regions, were conducted in the Amazonian rainforest and focused on dung beetles (Klein, 1989; Andresen, 2003; Spector & Ayzama, 2003; Feer & Hingrat, 2005; Gardner *et al.*, 2008; but, see Didham *et al.*, 1998; Uehara-Prado *et al.*, 2009).

Forest succession is accompanied with an increase in litter fall (Ewel, 1976) and tree diversity (Liebsch *et al.*, 2008), which accelerates the amount and complexity of leaf litter (Burghouts *et al.*, 1992). An increase in quantity (Jonsson & Jonsell, 1999; Barberena-Arias & Aide, 2003) and complexity (Tews *et al.*, 2004; Lassau *et al.*, 2005) of inhabited substrate often positively affects beetle diversity and composition. It is frequently traced back to increased resource availability (Gotelli & Colwell, 2001) and an extensive number of habitable niches (Klopfer & MacArthur, 1960). Furthermore, macro-fauna in or on soils is dependent upon microclimatic conditions (Martius *et al.*, 2004). In particular, soil moisture has a strong effect on species diversity and composition (Lassau *et al.*, 2005).

We investigated the recovery pattern of litter inhabiting beetles during natural forest regeneration, in soils differing markedly in moisture content in the Mata Atlântica (Atlantic Forest) of Brazil. To the best of our knowledge no comparable study, examining the effect of forest succession and soil type on litter beetles, has been conducted in the Brazilian Atlantic Forest, one of the most threatened tropical forest biomes in the world. Migration, industrialisation and urban expansion have resulted in only 11–16% of the original forest area remaining in small fragments of mostly secondary forests (Ribeiro *et al.*, 2009). Nevertheless, the Atlantic Forest biome still exhibits an enormous biodiversity, and its conservation is of extreme importance (Laurance, 2009). We addressed and tested the following hypotheses related to the response of litter inhabiting beetles to forest regeneration: (i) species density increases and species composition changes with forest age. (ii) Litter volume influences significantly species density and composition. (iii) Different soil types have different species composition and affect species density.

Methods

Study area and sites

The study was conducted in the coastal mountain range in Paraná, Southern Brazil, within the municipality of Antonina. The regional climate is classified according to Köppen as Cfa (humid subtropical, Peel *et al.*, 2007), with an annual rainfall of 2000–3000 mm, a wet season from September to April and a dry season from May to August. The average annual temperature is 20° C. The study sites were located in the Cachoeira Nature Reserve, owned by the Brazilian NGO Society for Wildlife Research and Environmental Education (SPVS) (Fig. 1). The reserve is located in the submontane forest zone (0–600 m above sea level). The natural vegetation is classified as humid submontane forest (IBGE 1992). Forest disturbances were caused mainly by buffalo grazing, cash crop plantations and selective logging. This has led to a mosaic landscape of mature and different-aged secondary forests embedded in a matrix of small settlements, farms and pastures.

We used a chronosequence approach to investigate the recovery of litter inhabiting beetles during forest regeneration. A chronosequence comprises three stages of secondary forest: Stage 1 (very young: ∼5 years after abandonment), Stage 2 (young: 12–15 years), Stage 3 (old: 35–50 years) and Stage 4 as a reference (old-growth forests: at least 100 years without anthropogenic impact). To investigate the influence of soil type on recovery patterns, chronosequences were studied on two contrasting soil types: cambisol and gleysol. Gleysols, unlike cambisols, are influenced by groundwater and have a seasonally high water level. Because the flat plains of the reserve were intensively anthropogenically used, old-growth forests are not found on the gleysol; therefore, they could not be included in the study design. Three replicate sites per forest stage/soil type combination were established and scattered throughout the reserve. The age after abandonment was estimated from information provided by long-time residents and from satellite photos taken in 1952, 1980 and 2002. Sites were located using local vegetation and soil data provided by the SPVS.

Sampling methods and beetle identification

Beetles were collected from June to July 2003 from 20 1-m^2 leaf litter samples taken at each site using a 1-m^2 frame. Samples were taken every 5 m along two parallel 50 m transects installed at least 50 m from the forest edge to minimise edge effects. The leaf litter was sieved through a 10-mm mesh. Beetles were extracted from the samples using the Winkler method (Besuchet *et al.*, 1987); Winkler bags were suspended for 3 days, which was suitable for a comparative survey of litter inhabiting beetles (Krell *et al.*, 2005). Leaf litter volume was measured by filling the coarse leaf litter in a graduated bucket, slightly compressing the foliage using a standard weight and then measuring the
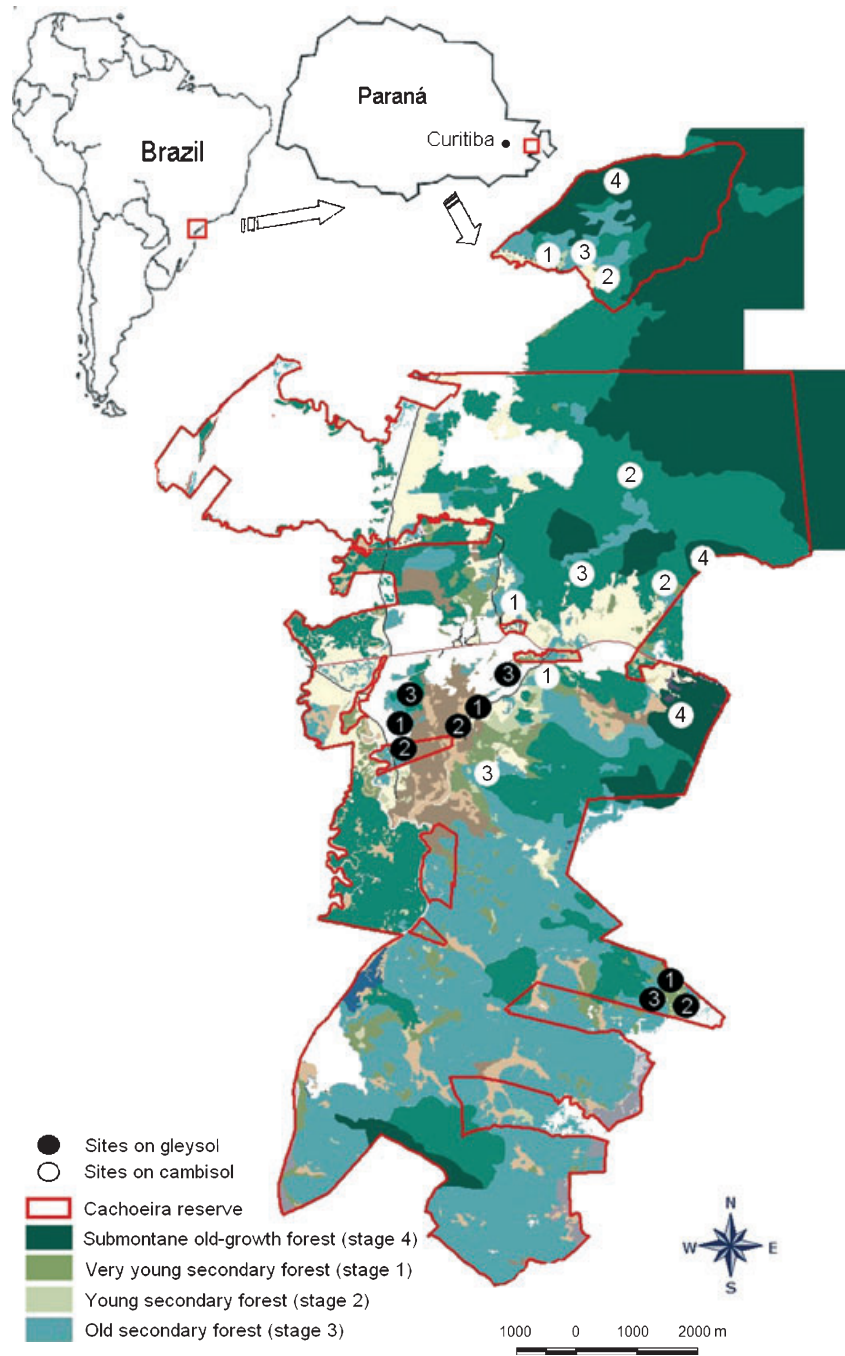
Fig. 1. Map of the study region, indicating the location of the study sites in the Rio do Cachoeira Reserve. Numbers indicate successional stages 1–4 (white circles: sites on cambisol, black circles: sites on gleysol).

depth of the litter. Beetles were identified to the family level using the keys from Lawrence *et al.* (1999). Nine beetle families [Carabidae, Curculionidae (with the exception of Scolytinae), Staphylinidae, Leiodidae, Endomychidae, Hydrophilidae, Cerylonidae, Eucinetidae, and Tenebrionidae] were further sorted into morphospecies (Oliver & Beattie, 1996; Barrat *et al.*, 2003) or species when possible. We refer to morphospecies as species. We chose these beetle families because: (i) they were sampled in high numbers. (ii) They are typical inhabitants of leaf litter. (iii) Taxono-

mists were able to study our material. We also differentiated between predators (Staphylinidae, Carabidae) and decomposers (Curculionidae, remaining five families). As we lacked data on the feeding behaviour of focal species, we determined trophic groups using data listed in Lawrence *et al.* (1999) and in the literature cited in Hanagarth and Brändle (2001). Accordingly, the decomposer group includes fungivorous, phytophagous, and saprophagous species. Voucher specimens were deposited in the Department of Zoology, University of Curitiba (UFPR).

Data analyses

Species data for all 20 sub-samples per site were pooled because individual catches were too small for reliable analyses. We compared species density rather than species richness between forest stages. This was due to the low species counts at several sites, which we considered a meaningful part of the response pattern. We standardised the observed species numbers by estimating total species numbers using an abundance-based non-parametric estimator (Jack 1) (EstimateS 8.0, Colwell, 2006). Patterns in species density were analysed conjointly for all beetle families and separately for Staphylinidae, Carabidae, Curculionidae and the remaining families using one-way analysis of variance (one-way ANOVA) and Fisher's LSD *post hoc* tests (SPSS 17.0.2, Chicago, IL, USA). Pearson correlations between species density of Staphylinidae, Carabidae, and Curculionidae were conducted to test for possible indicator groups reflecting overall species density. We examined the effect of litter volume, successional stage and soil type on species density with two-way ANOVA (SPSS 17.0.2). The effect of litter volume on species density was examined in analyses with and without litter volume as covariate. Additionally, we compared species richness between old-growth forest and old secondary forest using sample based rarefaction curves (EstimateS 8.0). We calculated relative evenness of abundance and counted the number of species unique to each forest stage⁄soil type combination. Unique species are defined here as those species represented by at least two specimens in a successional stage⁄soil type combination and no specimens in other combinations. We tested for differences in species composition among forest stages on both soil types using the multiresponse permutation procedure (MRPP) and visualised pattern of similarity in beetle assemblage composition with non-metric multidimensional scaling (NMDS) ordination. This was based on square root transformed data and the Bray-Curtis distance measure (PCOrd version 4.01, McCune & Mefford, 1999). We used a permutational multivariate analysis of variance (PERMANCOVA, Anderson, 2005) to examine the effect of successional stage (Stages 1–3), soil type and litter volume as covariate on an assemblage composition with 999 permutations of residuals in the full model, using square root transformed data and Bray-Curtis distances.

Results

Beetle fauna

A total of 3683 beetles, representing 35 families (Appendix 1), were collected from 420 m² leaf litter. Dominant beetle families were staphylinids (52.5%), curculionids (13%), scydmaenids (9%) and carabids (9%) together representing 83.5% of total counts. Fifteen families were represented only as singletons or doubletons; 2181 specimens of nine beetle families were determined to 256 species. The most species rich families were staphylinids (159 species), curculionids (39), and carabids (23). Fifty-seven per cent of all species were recorded as singletons or doubletons. Species accumulation curves did not reach an asymptote. The estimate of total species number (34–77%) indicated a moderate level of completeness (Table 1).

Species density and richness

Species density increased with forest age (cambisol: $P = 0.001$; gleysol: $P = 0.01$; $n = 3$; Fig. 2a). On cambisol,

Table 1. Diversity and abundance of leaf litter beetles along successional stages in the Atlantic Forest of Southern Brazil.

Parameter	Soil type and successional stage*						
	Cambisol				Gleysol		
	Stage 1	Stage 2	Stage 3	Stage 4	Stage 1	Stage 2	Stage 3
Number of families†	9.0 ± 2.6	9.7 ± 1.2	14.3 ± 4.2	15.3 ± 2.1	8.0 ± 2	9.3 ± 0.6	9.0 ± 1.0
Abundance (families)†	60.3 ± 25.5	106.0 ± 64.1	348.0 ± 238.5	390.3 ± 107.9	33.7 ± 8.1	172.3 ± 37.1	131.3 ± 77.2
Observed number of species†	16.7 ± 3.2	20.3 ± 3.5	57.0 ± 16.6	62.0 ± 9.2	8.3 ± 0.6	33.3 ± 5.9	29.7 ± 11.8
Abundance (species)†	38.7 ± 22.4	38.7 ± 16.5	237.0 ± 182.3	236.7 ± 101.2	12.3 ± 4.0	93.3 ± 26.6	70.3 ± 48.8
Estimated number of species‡	25.8 ± 3.0	34.6 ± 4.5	85.5 ± 20.2	89.5 ± 9.4	14.0 ± 2.2	50.4 ± 12.7	47.4 ± 18.5
Unique species	3	2	6	13	1	8	0
Completeness (%)§	34/52/57	47/62/61	56/64/56	66/75/77	72/65/67	57/68/75	63/63/61
Evenness (J')	0.86 ± 0.13	0.92 ± 0.05	0.86 ± 0.04	0.87 ± 0.04	0.96 ± 0.03	0.88 ± 0.02	0.92 ± 0.06

*Numbers represent different-aged forest stages comprising secondary forests of ∼5 years (stage 1), 12–15 years (stage 2), 35–50 years (stage 3), and old-growth forest (stage 4).

†Means of three replicate sites ($n = 3$). Sub-samples of each site were pooled. Number of species observed on 20 1-m² plots of forest floor.

‡Estimated total number of species (on 20 1-m² plots of forest floor) using the Jack 1 richness estimator with 100 randomisations without replacement.

§Percentage of Jack 1 estimate compared to observed number of species. Completeness is stated for every replicate site.
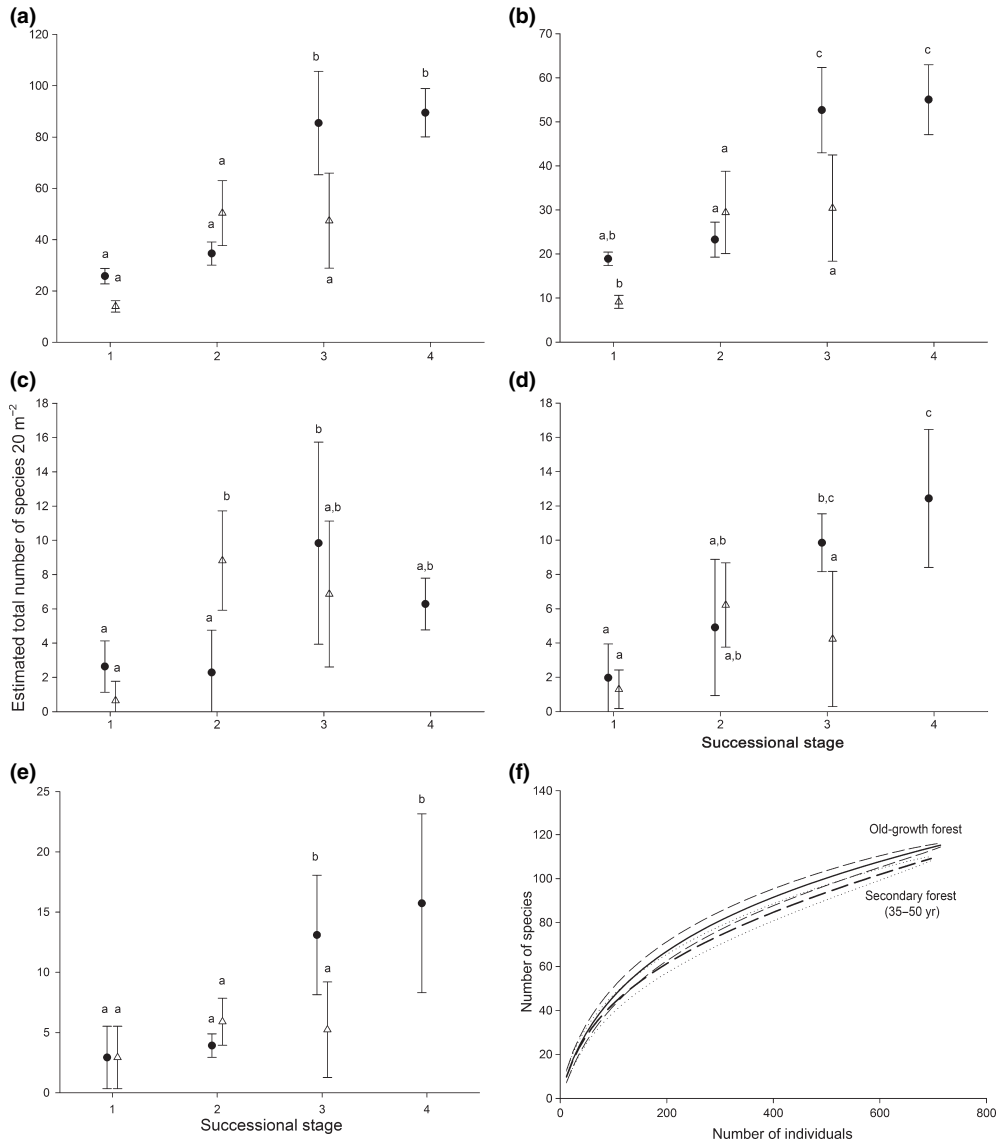
Fig. 2. Patterns of species density (a–e) and species richness (f) of secondary and old-growth forests. The mean estimated species density of different-aged secondary forests (stages 1–3) and old-growth forest (stage 4) were compared for all species combined (a) and for only staphylinids (b), carabids (c), curculionids (d), and for less-abundant beetle families belonging to the decomposer group (hydrophilids, tenebrionids, eucinetids, endomychids, leiodids, cerylonids) in a joint plot (e). Stages on cambisol (●) and gleysol (Δ) were analysed separately. Stages (*n* = 3) were tested among each other for statistical significance (LSD tests, *P* ≤ 0.05). In a–e, different letters indicate different means. (f) Sample based rarefaction curves of mature secondary forest (stage 3) and old-growth forest on cambisol, calculated for all three sites combined.

Stage 1 (very young) and Stage 2 (young secondary forest) did not differ significantly from each other (Fig. 2a). However, the total species density was convincingly lower than that of older forest stages (Fig. 2a). The species density of old secondary forest did not differ significantly from that of old-growth forest (Fig. 2a). The species density of Stage 1 was notably lower than that of Stages 2 and 3 on gleysol; on the other hand, the species density did not increase between Stage 2 and Stage 3 (Fig. 2). Predators (Fig. 2b, c) and decomposers (Fig. 2d, e) showed a similar pattern. We found meaningful effects of successional

stage and soil type on total species density (Table 2a). When litter volume was added as covariate to the model, soil type no longer significantly affected total species density (Table 2b). Sample based rarefaction curves of species richness showed no notable difference between old-growth forest and Stage 3 (old secondary forest, Fig. 2f). Evennesses between successional stages were similar and ranged from 0.86 to 0.96 (ANOVA, *P* = 0.76, *n* = 3; Table 1). The staphylinid density pattern showed the best correlation to overall species density (*r* = 0.93, *P* < 0.001).

Table 2. Results of two-way ANOVA on the effect of soil type and successional stage on species density. The effect of litter quantity was evaluated by calculating the effects of soil type and successional stage without considering litter quantity in the model (b) and by adding litter volume as covariate (a).

Source of variation	SS (type I)	d.f.	MS	F	P
(a)					
Soil type	4168.0	1	4168.0	18.8	0.001
Successional stage	8843.5	3	2947.8	13.3	<0.001
Soil type × successional stage	2165.3	2	1082.6	4.9	0.026
Error	2883.4	13	221.8		
(b)					
Litter volume	14702.7	1	14202.7	115.1	<0.001
Soil type	9.3	1	9.3	0.1	0.970
Successional stage	1343.4	3	447.7	3.5	0.010
Soil type × successional stage	471.3	2	235.6	1.8	0.020
Error	1533.6	12	127.8		

Litter volume

The mean leaf litter volume per site between samples and within replicates was highly variable. Litter volume changed significantly during forest regeneration ($P = 0.04$, $n = 3$; Fig. 3). The mean leaf litter volume of young secondary forests was lower than that of old secondary forests and old-growth forest.
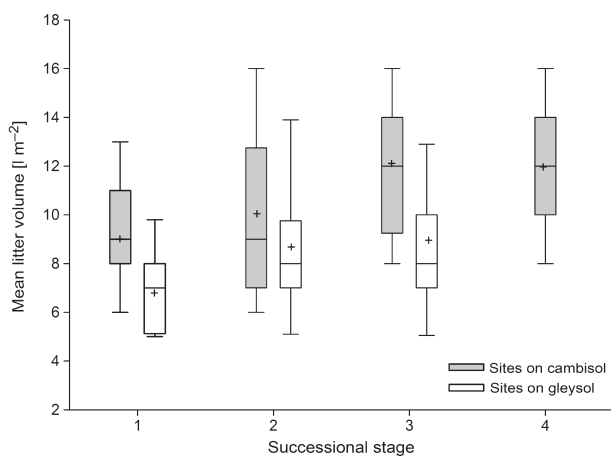

Fig. 3. Box plots of leaf litter volume per m² in different successional stage/soil type combinations in the Atlantic Forest of Brazil. The central horizontal line in the box marks the median of the values; the box edges the first and third quartile. The inter-quartile range within the box includes the central 50% of the values. The whiskers show the range of observed values that are not within the first and third quartile but not further away than 1.5 times the inter-quartile range from the hinges. Crosses are the arithmetic mean. Each box contains 20 values of three replicate sites, making a total of 60 values.

Litter volume was lower at gleysol sites than at cambisol sites, except for Stage 2. The increasing litter volume and increasing species density patterns were highly consistent with regard to successional stage and soil type.

Beetle assemblage composition

The species composition of litter inhabiting beetle assemblages differed among successional stages (MRPP, cambisol: $P = 0.015$; gleysol: $P = 0.01$; Fig. 3). Multidimensional scaling ordination grouped sites on gleysol separately from sites on cambisol (Fig. 4). Young forests (Stages 1 and 2) showed high heterogeneity. On cambisol, the assemblage composition of Stages 1 and 2 differed significantly from that of Stage 3 and old-growth forest (Stage 4; MRPP, $P = 0.03$). The assemblage composition of Stages 3 and 4 was less variable among sites and did not differ from each other (MRPP, $P = 0.89$). On gleysol, the assemblage composition of Stage 1 differed from that of Stages 2 and 3 (MRPP, $P = 0.02$). The assemblage composition was significantly affected by soil type ($P = 0.004$), successional stage ($P = 0.035$), as well as litter volume ($P = 0.001$).

Discussion

Patterns of species density and richness

The species density of leaf litter beetles in old-growth forests was much higher than that of secondary forests, 5–15 years after
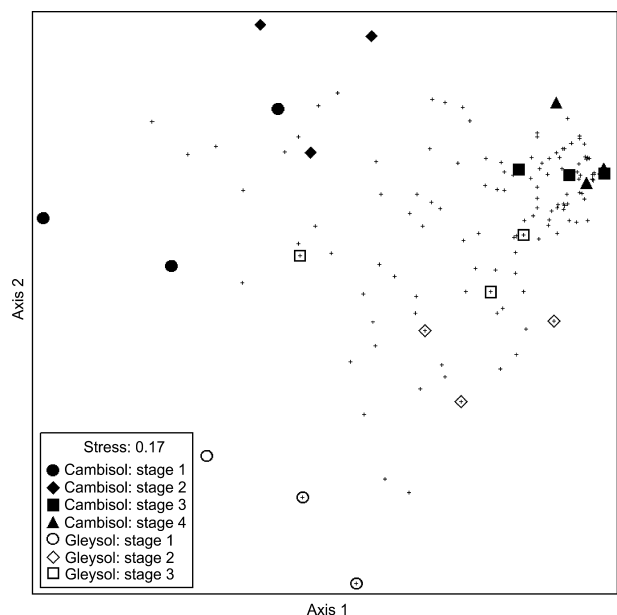

Fig. 4. Non-metric multidimensional scaling (NMDS) ordination of the leaf litter beetle assemblages, according to successional stage and soil type. Species are indicated with crosses. Successional stage/soil type combinations grouped closer together are more similar in species composition.

abandonment. This reveals a clear negative effect of deforestation on the diversity of the selected beetle families, as reported for many other taxa (e.g. Lawton *et al.*, 1998; Nichols *et al.* 2007; Bihn *et al.*, 2008). Moreover, the very low number of species in young forests, mostly found as singletons, demonstrates the unsuitability of these habitats for beetles inhabiting this niche in mature forests as well as for species well adapted to open habitats. Larger open habitats are not a natural component of the landscape; therefore, the invasion of open habitat species in deforested sites probably influences the recolonisation of leaf litter beetles very little in the area studied.

Old secondary forests of about 35–50 years already had species densities and richness similar to that of old-growth forest, indicating a rapid recovery during further forest regeneration. This result supports the conclusion of Dunn (2004) and Grimbacher *et al.* (2007) that species richness is the component of diversity with the highest recovery ability.

The recovery patterns of predators and decomposers did not differ significantly (Fig. 2b–e) with an almost linear relationship between their densities (see Gaston *et al.*, 1992). A direct predator/prey interaction seems insufficient to explain this pattern, as the abundance of predators clearly exceeds that of decomposers. The pattern can best be explained by a general cascading effect of lower trophic levels on the diversity of higher trophic levels driven by litter quantity (Barberena-Arias & Aide, 2003).

We found Staphylinidae to be the most abundant and species rich beetle family by far in our study sites, which is also found in nearby temperate forests (Marinoni & Ganho, 2003) and the Amazonian region (Didham *et al.*, 1998; Hanagarth & Brändle, 2001). The pattern of staphylinid density observed was strongly correlated with the pattern of overall beetle density. Thus, although their taxonomy is notoriously difficult, staphylinids may be a good biodiversity indicator of beetle assemblages in tropical forests.

Recovery of assemblage composition

Patterns of significant changes in species composition during forest regeneration were comparable to those of species density (Figs 2 and 3). Compared to the assemblages of mature forests, the assemblages of young forests were more similar to each other; however, the initial post-disturbance assemblages of the young forests still varied greatly. We suggest that this heterogeneity is caused by variable recolonisation scenarios, which are affected by differing vegetation structures. These in turn influence microclimatic conditions and litter quantity (Liebsch *et al.*, 2007), by proximity of native habitats (Pawson *et al.*, 2008) and by disturbance history (Saint-Germain *et al.*, 2005). Old secondary forests varied less in composition and were not distinguishable from old-growth forests. Grimbacher *et al.* (2007) found similar results; possible reasons for these observations were given as a longer time for beetle accumulation, a greater structural habitat complexity (Lassau *et al.*, 2005) and larger plant species richness (Haddad *et al.*, 2001). However, comparable studies still found large differences between old secondary forests and old-growth forests, emphasising a much longer time span for the recovery of ant (Dunn,

2004; Bihn *et al.*, 2008), amphibian/lizard (Gardner *et al.*, 2007a) and bird assemblages (Dunn, 2004; Barlow *et al.*, 2007b). We suggest four explanations for the fast recovery of leaf litter beetle assemblages, observed in our study. First, many litter inhabiting beetles are volant or have a high surface mobility, allowing them to disperse well. Second, the short generation time of beetles promotes rapid recolonisation of suitable habitats. Third, a quantity of leaf litter comparable to that of old-growth forest offers adequate microhabitats for most forest species. Fourth, large old-growth forest patches, which still exist in our study area, could serve as species sources for secondary forests, which feature conditions already suitable for forest species.

Sample adequacy and rare species

Rare species are an integral part of tropical insect assemblages (Novotny & Basset, 2000) as shown in many beetle studies in tropical forests (e.g. see Didham *et al.*, 1998; Grimbacher *et al.*, 2007). We only reached a moderate degree of sample completeness with many singletons, making it difficult to distinguish between random catches and distribution patterns of rare species. However, the reliability of our findings is supported by an almost identical pattern of additional chronosequences in a nearby reserve (only on cambisol), despite seasonal and spatial differences in sampling. Nevertheless, we found at least 13 'unique' species in old-growth forests that could not be statistically confirmed as indicators of old-growth forests. We suggest that probably more rare beetle species will be lost through deforestation than short-term studies are able to detect. Therefore, we stress the importance of maintaining old-growth forests to protect forest biodiversity.

Effect of soil type on the recovery pattern

The soil type strongly influenced the recovery pattern of species density and composition. Lower species densities in old secondary forests on gleysol compared to cambisol indicate that the harsh conditions on gleysol may restrict species establishment. Other studies have shown that high soil moisture negatively affects beetle diversity by influencing adult habitat selection and reproduction (Doube, 1983; Vessby & Wiktelius, 2003). However, the surprisingly similar pattern of species density and litter volume indicates that the amount of litter may be far more important for explaining the species density pattern than soil moisture. This assumption is supported by the observation that little additional variance is explained when leaf litter is added to the model (Table 2). Thus, soil type seems to affect species density indirectly by affecting litter quantity. Seasonal flooding that occurs on the gleysol sites may restrict the development of deep and complex litter layers; thereby, reducing the number of species, as reported for spiders (Uetz, 1976). However, soil type significantly affected assemblage composition even when litter volume was added to the model (Fig. 3). This indicated that the composition of assemblages contains information not reflected in species diversity metrics. A convergence towards

more similar assemblages in older stages suggests that the major difference in assemblage composition could be confined to the recolonisation process. This signifies that pioneers on gleysol and cambisol differ and fewer mature forest species occur on gleysol than on cambisol.

Conclusions

The study established that beetle species density increases and assemblage composition changes during forest regeneration. However, only mature secondary forests of 35–50 years seem to be suitable habitats for most litter inhabiting beetle species. These mature secondary forests can be considered to contribute substantially to the maintenance of forest species, at least when old-growth forests remain nearby. Younger forests, up to 15 years after abandonment, showed low species densities even though they are situated in the immediate vicinity of an old-growth forest and feature an almost forest like structure.

Litter quantity was strongly correlated with species density and seems to reflect species density on both gleysol and cambisol soils. Thus, litter volume may be an important aspect of priority sites for conservation if the goal is to maintain a high density of beetle species. It is likely that insects will rarely be the primary target of future regional conservation strategies; thereby, causing litter quantity to be a valuable interface between the preservation of biotopes and the conservation of insects. However, it is debatable whether or not the addition of leaf litter, in initial regeneration stages, is an efficient tool for accelerating the recovery of leaf litter beetles. Nakamura *et al.* (2009) mentioned positive effects of mulching for the recolonisation of ants and points out the necessity of a fully closed canopy to suppress the invasion by pastoral species. In our study region a competition with pastoral species does not seem to limit the recolonisation of forest species; therefore, addition of leaf litter could be efficient even in the initial stages, when the canopy is not yet closed. However, the quantity of habitable substrate was not in itself sufficient to predict the structure of litter inhabiting beetle assemblages. Conditions related to soil type, especially if the soils differ dramatically, must be considered if highly diverse soil-related insect communities, such as beetles, are to be integrated into conservation strategies.

Acknowledgements

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Appendix 1

Beetle families and their abundances found in different successional stages (stage 1: ∼5 years; stage 2: 12–15 years; stage 3: 35–50 years after abandonment and stage 4: old-growth forest) in the Rio do Cachoeira Reserve, Paraná, Brazil.

Beetle family	Soil type and successional stage						
	Cambisol				Gleysol		
	Stage 1	Stage 2	Stage 3	Stage 4	Stage 1	Stage 2	Stage 3
Staphylinidae	69	196	552	562	67	287	220
Curculionidae	39	18	132	145	6	73	67
Scydmaenidae	13	10	99	148	7	26	40
Carabidae	15	9	136	124	1	30	23
Ptiliidae	12	45	17	54	3	52	6
Hydrophilidae	3	1	33	28	4	31	17
Eucinetidae	–	16	19	18	–	1	3
Chrysomelidae	13	13	7	1	2	5	2
Tenebrionidae	6	2	9	15	1	6	2
Cerylonidae	2	–	15	12	–	–	7
Leiodidae	1	–	13	14	1	1	1
Nitidulidae	2	2	2	13	–	2	1
Endomychidae	–	–	1	18	–	–	–
Coccinellidae	1	–	2	6	–	–	1
Hydraenidae	–	–	–	–	3	1	4
Scarabaeidae	–	–	2	2	–	–	–
Corylophidae	1	–	2	–	–	–	–
Zopheridae	–	2	–	–	–	1	–
Elateridae	–	–	1	1	1	–	–
Melandryidae	–	–	1	2	–	–	–
Anthicidae	1	–	–	1	–	–	–
Scirtidae	–	1	–	–	1	–	–
Cerambycidae	–	1	–	1	–	–	–
Ptilodactylidae	–	1	–	1	–	–	–
Lagriidae	–	–	–	–	2	–	–
Languridae	1	–	–	–	–	–	–
Limnichidae	–	1	–	–	–	–	–
Laemophloidae	–	–	1	–	–	–	–
Erotylidae	–	–	1	–	–	–	–
Trogossitidae	–	–	–	1	–	–	–
Cneoglossidae	–	–	–	1	–	–	–
Clambidae	–	–	–	1	–	–	–
Dytiscidae	–	–	–	–	1	–	–
Lycidae	–	–	–	–	–	1	–
Lampyridae	–	–	–	–	1	–	–
Families	15	15	20	23	15	14	14
Abundance	179	308	1045	1169	101	487	394