

The impact of forest management on litter-dwelling invertebrates: a subtropical–temperate contrast

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Abstract Land use intensification in forests is a main driver of global biodiversity loss. Although historical state of land use differs between subtropical and temperate zones, gradients of land-use intensities similarly range from unmanaged to very intensively managed forests. Irrespective of similar land use forces in both climate zones, comparative studies on land use effects are still rare. Such studies are, however, promising in discovering more general impacts and geographical specifics of land use intensification. We studied litter-dwelling invertebrates along a gradient of increasing land use intensity in subtropical forests in Southern Brazil and temperate forests in Central Europe using similar sampling designs. Effects of land use intensity on the entire community were analyzed on the level of orders and feeding guilds. In both climate zones a similar number of individuals were caught when standardized to 100 pitfall trap days, but taxa richness was higher in the subtropics. Moreover, community composition differed between both climate zones. In both regions, land use intensity did not affect taxa richness, but invertebrate abundance was affected in opposite ways; while increasing land use intensity resulted in a decrease of invertebrate abundance in the subtropics, an increase was observed in the temperate zone and this was mostly consistent regarding different feeding guilds. Management practices should take into account that the effect of land use intensity on biodiversity can differ drastically among climatic regions.

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Introduction

Increasing land use intensity and even more important land use change is known to be a major driver of biodiversity loss (e.g. Sala et al. 2000). This is particularly true for forest ecosystems. In tropical forest ecosystems, land use change by deforestation (e.g. by burning forests or extensive logging) is responsible for most of biodiversity loss (Maass 1995; Castano-Meneses and Palacios-Vargas 2003; Asner et al. 2005). However, not only forest destruction can have detrimental impact on tropical species richness but also its replacement by short-rotation plantations of single species (Chung and Epperson 2000; Fitzherbert et al. 2008). European temperate forests have been managed for several hundred years, often using elaborated management regimes. Nevertheless, temperate forestry can also have detrimental effects on forest biodiversity, for example, managed forests often lack some of the specific fauna typical of pristine forests, e.g. saproxylic Coleoptera species (Speight 1989). In recent years, however, modern forest management strategies increasingly recognize the need for the conservation of biodiversity and include a number of measures aimed to increase the number of species in forests, e.g. by avoiding large scale clear-cuts in age-class forests or increasing dead wood amount in forests. Such approaches exist in both temperate and tropical ecosystems and the success of such measures is still being assessed (Lindenmayer and Franklin 2002; Cyranoski 2007; Fonseca et al. 2009a).

The discussion on how to sustainably manage forests appears to be conducted separately for temperate and tropical forest ecosystems. One reason for this may be the different state of management in the different regions. While overall tropical forests are still affected by land use change, characterized by a high destruction rate with concomitant high loss of biodiversity, many temperate forests were deforested a long time ago and thus change in land use intensity and species composition has become more important in this climatic zone. As a consequence, the major issue in the tropical regions appears to be the halt of forest destruction while in the temperate regions a re-conversion into more diverse forests, e.g. from conifer forests to broad-leaved forests, is being discussed. Nevertheless, the basic question is the same for all systems: how to best combine the production of timber with the conservation of biodiversity and associated ecosystem services? In particular, a pressing question today is the role of plantations in sustainable forest management (Paquette and Messier 2009). Studies approaching this question for both temperate and tropical forest ecosystems are rare.

Tropical-temperate comparisons classically focus on the differences in the main drivers of biodiversity in the different systems, e.g. to explain the latitudinal gradient in biodiversity (e.g. Pianka 1966; Schowalter 1995; Takeda and Abe 2001; Hillebrand 2004; Novotny et al. 2006). The state of this discussion was summarized in a recent meta-analysis (Hillebrand 2004), that corroborated the universal decrease in diversity with increasing latitude, but also pointed out that there are subtle but important differences among different habitats and taxa in the slope of the relationship, and the lack of a consensus on the ultimate cause of the gradient. When directly comparing the diversity of similar habitats across latitudinal gradients, earlier studies tended to focus on particular taxa (Kusnezov 1957; Stanton 1979) or interactions (Jeanne 1979), while newer studies have had a broader focus, e.g. by studying differences in community structure (Schowalter 1995; Takeda and Abe 2001). For species-rich groups such as invertebrates measuring overall biodiversity in terms of species richness within an area is barely possible (Williams and Gaston 1994), and the use of a higher

taxonomic richness has been advocated for comparisons, which was reported as a good predictor for species richness in different regions of different vertebrate and invertebrate groups (Williams and Gaston 1994; Baldi 2003).

In this study we investigated if similar gradients in land use intensity, found in subtropical forests in Southern Brazil and in temperate forests in Central Germany, produce similar effects on the community of litter-dwelling invertebrates. The studied gradient ranged from unmanaged forests (*Araucaria* forests in Brazil, beech forests in Germany), selective logging (exclusively in Germany), to age-class plantations of the dominant species of the natural forests (i.e. *Araucaria* in Brazil and beech in Germany), to plantations of exotic species in Southern Brazil (eucalypt and pine) and species non-natural to the site in Central Germany (spruce), chosen to maximize the timber production. In particular, we tested how the climatic region interacted with land-use intensity to determine total abundance, higher-level taxonomic composition, and the guild structure of litter-dwelling invertebrates.

Methods

Land use gradients in Brazil and Germany

The land use gradient in both regions comprises four classes of intensity in both climate zones from low (class 1) to high land use intensity (class 4). In the subtropics, the gradient ranged from unmanaged Atlantic Forest dominated by *Araucaria angustifolia* (UA; class 1), old plantations of *Araucaria angustifolia* (PA, class 2), old exotic tree plantations of *Pinus taeda*/*Pinus elliotti* (PP, class 3), to relatively young plantations of the exotic *Eucalyptus saligna* (PE, class 4). In the temperate region, the gradient ranged from unmanaged beech forests dominated by *Fagus sylvatica* (UB; class 1), to selection-cutting beech forest (SB; class 2), plantations of beech (PB; class 3), and plantations of exotic spruce, *Picea abies* (PS; class 4). For each one of the in total 60 sites, we defined a permanent plot of one hectare (100 × 100 m). The different forest types are described in more detail below.

Subtropical forests in Brazil

In Brazil, the study was conducted in the São Francisco de Paula National Forest, Rio Grande do Sul State, Brazil (29°23′–29°27′S, 50°23′–50°25′W). The National Forest, with 1607 ha, is located in a region that was originally dominated by *Araucaria* forest which constitutes the southernmost portion of the Brazilian Atlantic Forest (Ribeiro et al. 2009). The climate is subtropical, with a mean annual temperature of 18.5°C and a mean annual rainfall of 2225 mm (Backes 1999). The canopy is frequently dominated by *Araucaria angustifolia*, but has also the presence of a large number of Myrtaceae, Lauraceae and Fabaceae. The National Forest is a conservation unit of sustainable use, being a heterogeneous mosaic landscape comprising fragments of *Araucaria* forest mixed with patches of plantations of the native species *Araucaria angustifolia* and exotic species of the genera *Eucalyptus* and *Pinus*. In the national forest tree stands are relatively small. The rotation periods are much longer than the ones adopted by commercial plantations and a dense and rich understorey is allowed to develop. Also, the stands developed in the absence of fire and agrochemicals (Fonseca et al. 2009b).

In the Brazilian sampling design, each of the four different land use classes was replicated three times, resulting in a total of 12 sites. The three sites within one habitat type represented different historical backgrounds. The *Araucaria* forest site UA2 was the most

pristine whereas the sites UA1 and UA3 suffered slightly from cattle invasion and selective logging before the national forest establishment as a conservation unit in 1965. The plantations of *Araucaria*, pine and eucalypt were established in areas previously used for cattle range and agriculture. *Araucaria* plantations were established in 1947 (PA2 and PA3) and in 1959 (PA1), those of pine in 1965 (PP1, *Pinus elliottii*), in 1968 (PP2, *P. taeda*), and 1972 (PP3, *P. taeda*) and the plantations of *Eucalyptus saligna* were established in 1972 (PE1), 1988 (PE3) and 1994 (PE2). For more information about the study site, see Fonseca et al. (2009a).

Temperate forests in Germany

In Germany, the study was conducted in the area of Hainich-Dün, a range of hills in the North-West of Thuringia (51°23′–50°56′N, 10°10′–10°46′E). The mean annual temperature is 6.5–8°C and the mean annual precipitation rate is between 500 and 800 mm (Fischer et al. 2010). With a 16,000 ha area, the Hainich is one of the largest closed forest areas in Germany and is dominated by broad-leaved trees.

The Hainich National Park is located at the southern edge of this region and comprises unmanaged beech forests. It was founded in 1997 and covers an area of 7,600 ha. The current area of the national park was a protection zone for a military training range from 1945 until 1990. The national park is characterized by unmanaged, uneven-aged (up to 250 years) mixed deciduous forest (*Fagus sylvatica*, with *Fraxinus excelsior*, *Acer pseudoplatanus* and others). The core area of the national park where there was no forest management since at least 40 years, comprises 261 ha and is unique for Germany in terms of its age, structure and extent.

In the wider Hainich-Dün region, a broad spectrum of differently managed beech forests occurs, including selection-cutting and age-class forests. In the selection-cutting beech forests only selected trees are cut and trees in the gaps recruit from seed fall. This type of management creates a permanent forest of uneven-aged stands of different tree species with different age. Forests gaps occur when individual trees are cut. In contrast, beech age-class forests in the Hainich-Dün region are characterized by homogeneous even aged stands of different developmental stages (age-classes). Rotation time for beech age-class forest (plantations) is around 160 (± 30) years. Because of a change in management practices, the younger age-class forests did not originate from clear-cuts with subsequent planting, but included both natural seedling recruitment and the preservation of some mature trees (120–180 years) that were cut only once the young cohort reached an age of somewhere between 10 and 20 years. In both the unmanaged beech forests and the beech age-class forest stands are characterized by an almost closed canopy structure without gaps. These shady conditions result in a nearly complete absence of a shrub layer.

Spruce (*Picea abies*) does not occur naturally in the Hainich regions. Stands are rare in the Hainich region as experience has shown that spruce, which is grown for timber in large areas of Germany, does not grow well on the limestone and as a consequence stands become unstable with age. In the majority of cases the current spruce stands are afforestations of former agricultural sites that were cleared of diverse beech forests in the more distant past. Rotation time for spruce is around 100 years and selected stands were between 58 and 80 years old.

The German sampling design involved, in total, 48 sites. For unmanaged beech forests (UB), 11 sites were selected, all of them located in the Hainich national park. There were 13 sites of selection-cutting beech forest (SB), 20 sites of beech plantations (PB) and four plantations of spruce (PS) (Fischer et al. 2010). In selected stands the dominant tree species

(beech, spruce) made up at least 70% of total tree basal area. For beech plantations, different age-classes were chosen while for spruce the selection was severely limited due to the small number of stands in the region.

Invertebrate sampling

Invertebrates were sampled by pitfall traps in both regions. In Brazil, three sampling units were randomly installed in each plot, each sampling unit consisting of five pitfall traps (four in each corner of a 25 m² square and one in its center). The pitfall traps were transparent plastic cups (Ø 7.5 cm, height 10.5 cm) that were buried into the soil with the rim at level to the soil surface. Sampling took place in August 2003 (winter) and March 2004 (summer). Pitfall traps remained active for eight consecutive days during each sampling period. Total sampling effort per site was 240 pitfall trap-days. In Germany, invertebrates were collected by only two randomly located pitfall traps (Ø 15 cm, for general trap design see Lange et al. (2011)) per site. Sampling was continuous from mid of April to mid of October 2008 (185 days) during the entire season. Total sampling effort per site was 370 trap-days.

We are aware of the limitations of pitfall trap samples which have been discussed comprehensively (an overview is given in Southwood and Henderson 2000). In our study pitfall traps differed slightly in design and timing of placement between both regions. We minimized these differences by standardizing the catches (see below) and thus, we believe that pitfall traps are the method of choice for comparing litter-dwelling arthropod communities on projects involving large spatial and temporal scales. Due to its temporal integrative character and the easiness to produce standardized protocols even among research groups, pitfall traps is the most commonly used method for sampling litter-dwelling arthropods and recommended by many authors (e.g. Duelli et al. 1999; Southwood and Henderson 2000).

Taxonomic and guild classification

The invertebrates of both regions were classified into 36 taxonomic units. Most units correspond to the order level, but a few are classes (e.g. Gastropoda) or families (e.g. Formicidae). Although Nematodes were found in both study regions, they were not included in the analysis, because in temperate region there was no data available concerning their abundances.

We classified most taxa into four specialized feeding guilds (if >90% of species fitted the guild): (1) detritivores—Amphypoda, Archaeognatha, Blattaria, Collembola, Diplopoda, Isopoda, Isoptera, Oligochaeta, (2) herbivores—Gastropoda, Hemiptera: Homoptera, Lepidoptera, Orthoptera, (3) parasites—Hirudinae and Hymenoptera, (4) predators—Araneae, Chilopoda, Scorpionidae, Mantodea, Neuroptera, Odonata, Opiliones, Pseudoscorpiones, Megaloptera, Raphidioptera, and Tricladida. The remaining taxa were defined as being (5) omnivores—Acarina, Coleoptera, Dermaptera, Diptera, Hymenoptera: Formicidae, Hemiptera: Heteroptera, Mecoptera, Plecoptera, Psocoptera, Thysanoptera, and Trichoptera.

Data analysis

For analyses, sampling effort was standardized to 100 trap-days per site for both regions. Abundance data were log transformed ($\log_{10} x + 1$) to obtain normal distributed error

structure and to stabilize the variances. Taxonomic richness was calculated as the total number of taxonomic units. We also calculated rarefied taxonomic richness after standardizing for sampling effort with the use of the software R 2.11.0 (R Development Core Team 2010). For calculating rarefied taxa richness we used the function *rarefy* within the *vegan* package (Oksanen et al. 2010).

A two-way factorial ANOVA was used to test the effect of region and land use intensity on abundance, absolute and rarefied taxonomic richness, as well as guild abundances, using a Type 1 sums of square. In both regions, intensity levels were coded 1–4. Assumptions of ANOVA were checked and data transformed as necessary. Differences in taxonomic and guild composition between region and land use intensity were analyzed by principal component analysis (PCA). Statistical analyses were carried out using SYSTAT (2004).

Results

Abundance and taxonomic composition

Overall, we recorded 354,175 individuals from 36 taxonomic groups. In the twelve subtropical sites, a total of 45,479 individuals from 31 taxa were collected while in the 48 temperate sites, we collected 308,695 invertebrates of 27 orders. Considering the standardized sampling effort of 100 trap-days, subtropical sites ($N = 12$) had an average of 1579.1 ± 174.7 (SE) individuals from 23.0 ± 0.6 (SE) (rarefied 21.3 ± 0.5) taxa while the temperate sites ($N = 48$) had 1761.4 ± 99.2 (SE) individuals belonging to 18.7 ± 0.2 (rarefied 15.3 ± 0.2) taxa.

The dominant taxa in the subtropical region, comprising 79% of all individuals, were Collembola, Coleoptera, Formicidae, and Diptera, while the four most abundant taxa in the temperate sites were Acarina, Collembola, Coleoptera, and Diptera, comprising 89% of the sampled individuals (Fig. 1). Nine taxonomic groups were exclusively recorded in the subtropical region, while the temperate region had only five exclusive groups.

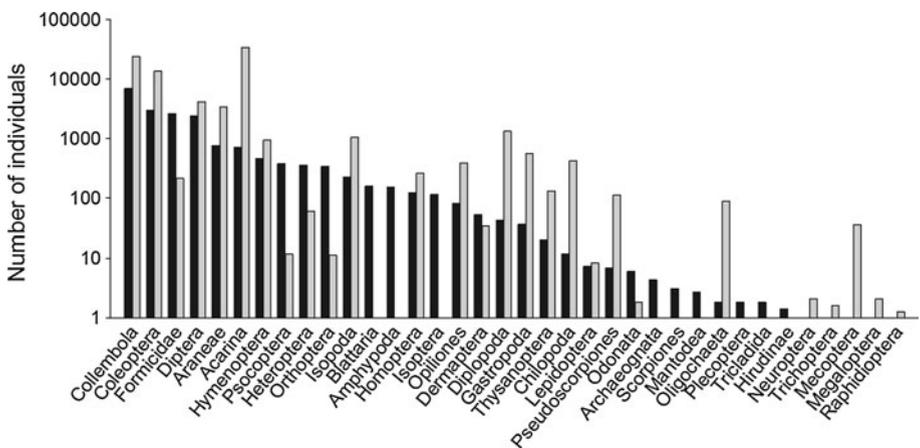


Fig. 1 Rank-order abundance of taxa collected in forests in Brazil and Germany, ordered by abundance of the subtropical taxa. Abundances were standardized for 100 trap-days per site. *Black bars* represent sites in the subtropics, *grey bars* sites in the temperate region

The impact of land use on the abundance of invertebrates differed between the two climatic regions (interaction land use*region: $F_{3,52} = 5.26$, $P = 0.003$). While in the subtropical region, the abundance of invertebrates decreased with increasing land use intensity, the abundance increased in the temperate region (Fig. 2a, b).

Total and rarefied taxonomic richness was higher for the subtropical sites than for the temperate sites (absolute, $F_{3,52} = 74.9$, $P < 0.001$; rarefied, $F_{3,52} = 129.0$, $P < 0.001$, variables square-root transformed). In the subtropical sites, taxonomic richness tended to decrease with increasing land use intensity, although plantations of *Eucalyptus* exhibited high values. In contrast, for the temperate sites, absolute and rarefied taxonomic richness were independent of land use intensity (Fig. 2c, d). For absolute taxonomic richness the interaction between land use and region was significant ($F_{3,52} = 3.8$, $P < 0.015$), while in the case of rarefied richness the interaction was marginally non-significant ($F_{3,52} = 2.1$, $P = 0.10$) and the main effect of intensity was also not significant ($F_{1,52} = 1.0$, $P = 0.39$, variables square-root transformed).

The taxonomic composition of the invertebrate communities differed between subtropical and temperate sites (Fig. 3). Furthermore, the taxonomical composition of invertebrates varied more widely among the subtropical sites than among the temperate sites, as judging by the greater spread of the subtropical sites along the three axes. The PCA indicated that subtropical sites have higher values along the first axis (explaining 27.6% of the total variation) which is positively correlated to the abundance of Isoptera (0.860), Psocoptera (0.853), Diptera (0.849), Formicidae (0.845), Orthoptera (0.834), Blattaria (0.800), Dermaptera (0.778), Hymenoptera (0.753), Heteroptera (0.753), Odonata (0.691), Escorpionidae (0.690), Lepidoptera (0.651), and negatively correlated to the

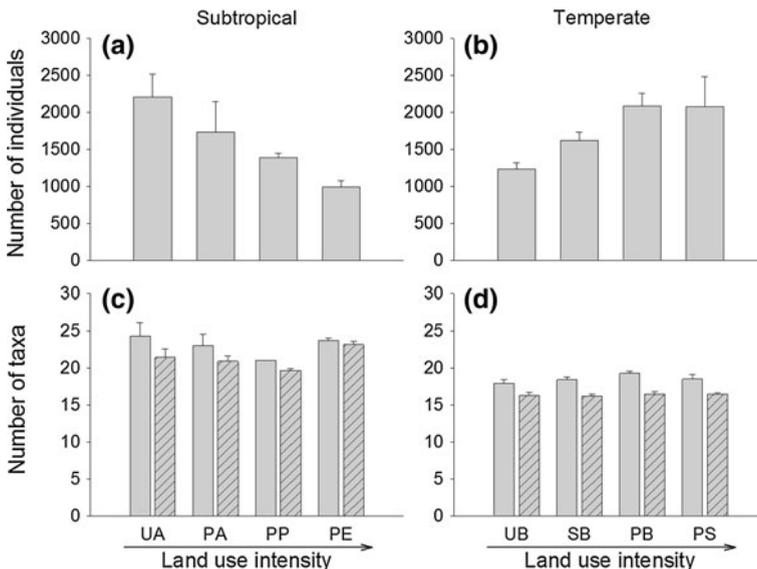
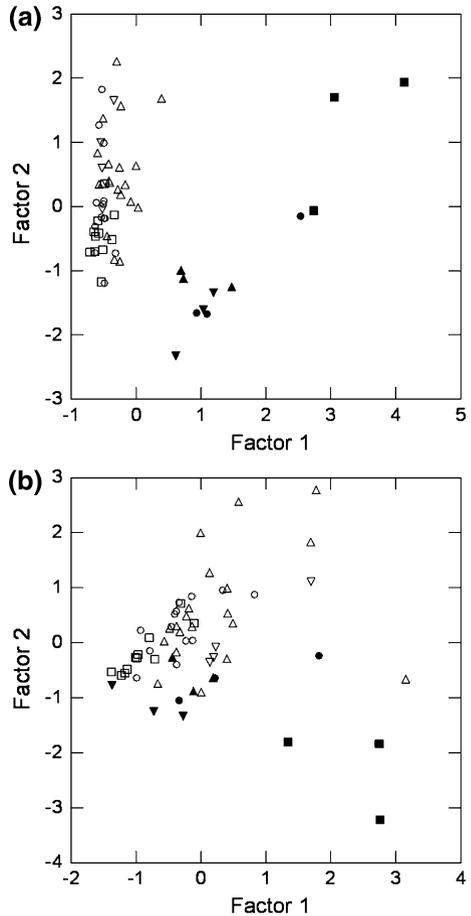


Fig. 2 Effects of land use on abundance and order richness of invertebrates in the subtropics and temperate region. The sampling effort per site was standardized to 100 trap-days. Land use intensity increases from left to right. Land use types in subtropics: unmanaged Araucaria forest (UA), plantations of Araucaria (PA), pine (PP) and of Eucalyptus (PE); in temperate region: unmanaged beech forest (UB), selection-cutting beech (SB), plantation (age-class forest) of beech (PB) and of spruce (PS). In c and d hatched bars are rarefied species richness

Fig. 3 Ordination diagrams of litter-dwelling invertebrate communities from 12 subtropical communities (closed symbols) and 48 temperate sites of different land use intensities. **a** Ordination based on 36 taxonomic units. **b** Ordination based on five feeding guilds. Land use types in the subtropical region are: unmanaged *Araucaria* forest (UA, filled square), plantations of *Araucaria* (PA, filled circle), *Pinus* (PP, filled triangle), and *Eucalyptus* (PE, filled inverted triangle). Land use types in the temperate region are: unmanaged beech forest (UB, square), selection-cutting beech (SB, circle), age-class plantations of beech (PB, triangle), and plantations of spruce (PS, inverted triangle). For the meaning of each axis, see text

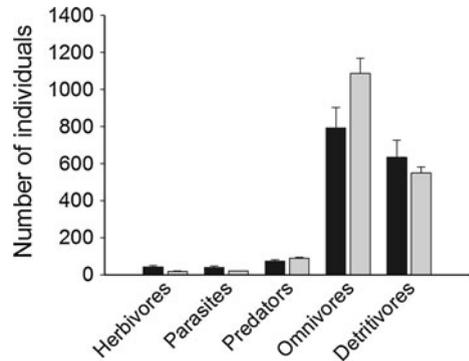


abundance of Gastropoda (-0.660), Oligochaeta (-0.580) and Diplopoda (-0.501). The second PCA axis, explaining respectively 10.1% of the total variation, was important to discriminate among different land uses within the subtropical region. Unmanaged *Araucaria* forest had higher values along the second axis when compared to the more intense land uses, indicating the predominance of Coleoptera (0.727), Isopoda (0.631), Araneae (0.618) and Diplopoda (0.519). For the temperate region, the different land uses were largely overlapped along the two main axes. The third PCA axis, that explained only 6.7% of the total variation, also did differentiate among different land uses. A non-parametric multidimensional scaling analysis showed very similar results compared with the PCA.

Guild abundance and structure

The relative abundance of the feeding guilds was quite similar between the two climatic zones although a multivariate comparison showed that feeding guild composition differed between the tropical and temperate regions (MANOVA, Pillai's trace $F_{5,54} = 13.2$, $P < 0.001$, Fig. 4). Overall, most invertebrates were omnivores (59.6%) and detritivores (32.8%), followed by predators (5.0%), parasites (1.4%) and herbivores (1.3%).

Fig. 4 Relative abundance of the feeding guilds in the subtropics and the temperate zone. *Black bars* represent sites in the subtropics, *grey bars* sites in the temperate region



Different feeding guilds tended to show similar responses to land use but responses differed between regions. The interaction between land use and region was significant for the abundances of detritivores ($F_{3,52} = 4.1$, $P = 0.011$), herbivores ($F_{3,52} = 5.0$, $P = 0.004$), parasites ($F_{3,52} = 12.7$, $P < 0.001$), omnivores ($F_{3,52} = 5.2$, $P = 0.003$) and predators ($F_{3,52} = 5.0$, $P = 0.004$, all abundances log-transformed).

In the subtropics abundances of guilds decreased with increasing land use intensity, while in the temperate region the opposite pattern was found (Fig. 5). In the subtropics all feeding guilds were most abundant in unmanaged *Araucaria* forests (except detritivores) and least abundant in *Eucalyptus* plantations (except herbivores). Detritivores showed relatively high abundances in the *Araucaria* plantations and predators, omnivores in the pine plantations. In the temperate region, detritivores, herbivores, and parasites were most abundant in spruce plantations. In beech forests, there was an increase of abundances with increasing land use intensity in all feeding guilds, except for the herbivores which showed nearly the same numbers of individuals in all beech forests.

Feeding guild structure differed between both regions and land use types within regions, as evidenced by a PCA analysis (Fig. 3b). The first axis, explaining 45.2% of the total variance, reflected the abundance of parasites (0.759), predators (0.728), and herbivores (0.699). The second axis, explaining 22.4% of the total variation, reflected positively the abundance of omnivores (0.584) and negatively the abundance of herbivores (−0.608). Subtropical and temperate sites had different guild structures, mostly due to the higher abundance of herbivores and lesser abundance of omnivores in the subtropical region. Unmanaged *Araucaria* forest sites differed from the other land uses due to their higher value along the first axis. In the temperate region, the age-class beech forest was the most heterogeneous in terms of guild structure but the different land uses were relatively similar in relation to the guild structure.

Discussion

Contrasting land use histories

Brazil and Germany are in two distinct phases in relation to the use of their forestry resources. Brazil has one of the largest and oldest native tropical forests in the world, despite deforestation still leading to losses of more than seven thousand square kilometres a year (INPE 2004). Additionally, Brazil has one of the strongest forestry industries, with

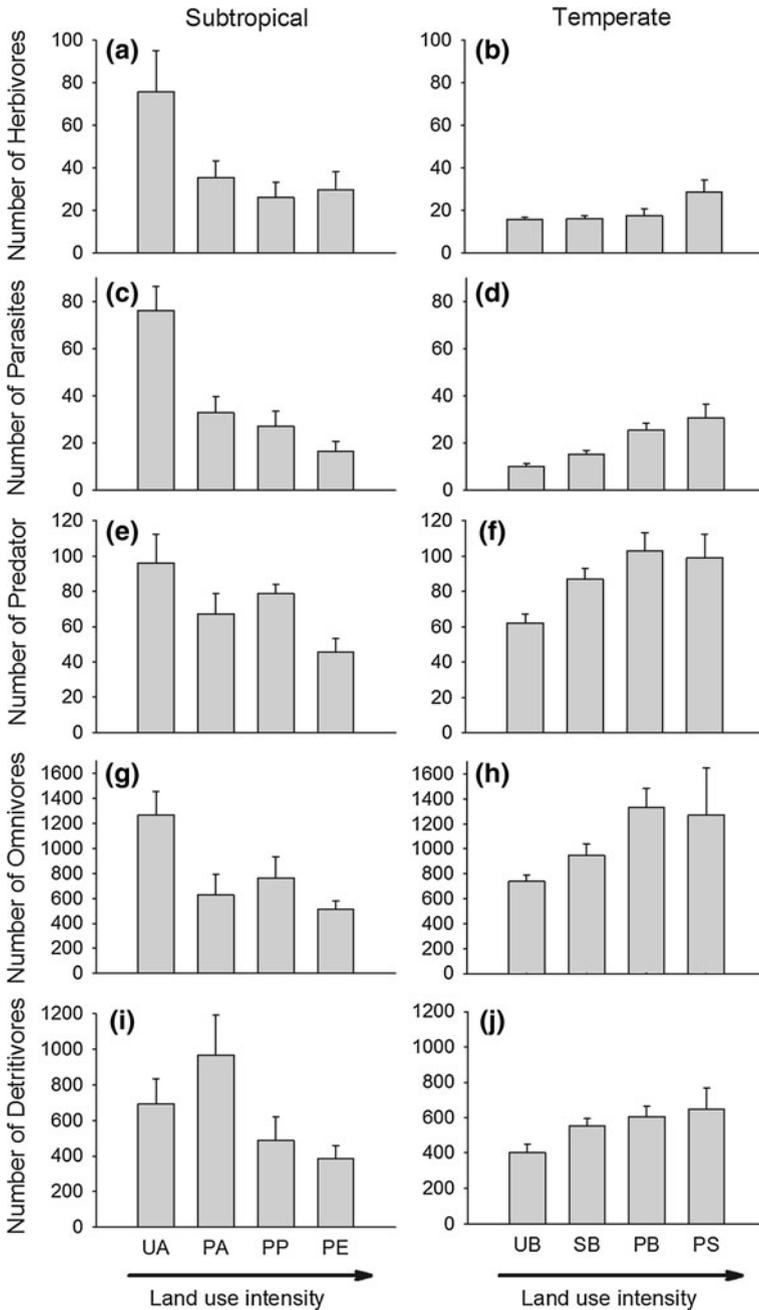


Fig. 5 Number of individuals in different feeding guilds and in the subtropical and temperate region along the gradients of land use intensity. Land use types: subtropics unmanaged *Araucaria* forest (UA), plantations of *Araucaria* (PA), pine (PP) and of *Eucalyptus* PE), temperate region: unmanaged beech forest (UB), selection-cutting beech (SB), plantation (age-class forest) of beech (PB) and of spruce (PS)

more than five million hectares of economically-managed exotic tree monocultures strictly designed to optimize timber production (Bacha and Barros 2004), but yet little experience in ecological management (Fonseca et al. 2009a). In contrast, the natural forests in Germany were formed after the last glacial period, about ten thousand years ago. However, they have been under strong human influence since at least the second half of the sixth millennium BC. (Rüther and Walentowski 2008). Nowadays basically all forested area has had some form of management (Ellenberg 1988; Rüther and Walentowski 2008). While in Brazil the conservation paradigm is still basically restricted to the conservation of “pristine areas”, conservation of Germany biodiversity relies on the protection of forest areas considered to have had comparatively little human influence (e.g. in national parks), and on introducing practices of ecological management into management practices. We believe that these historical differences are probably behind the contrasting patterns of land use intensity effects on litter-dwelling invertebrates in the two regions.

Despite South American forests have a long history, paleoecological evidences indicate that *Araucaria* forest replaced natural grasslands only during the initial Late Holocene period (4320–1100 cal year BP) due to the establishment of a warmer and wetter climate (Behling et al. 2004). Although, the presence of indigenous populations of the Jê language stock for at least fourteen centuries (Schmitz 2009), the *Araucaria* forest remained relatively untouched until the First World War. With the impossibility for Europe to commercialize pine wood from Riga (Letónia/Latvija), a strong timber industry progressively got established in the region due to the high quality of the *Araucaria angustifolia* wood (Mähler and Larocca 2009). Nowadays, only 12.6% of the 25,379,316 ha previously occupied by *Araucaria* forest remains intact (Ribeiro et al. 2009). The *Araucaria* forest remnants, however, still hold a high biodiversity (Fonseca et al. 2009b). In relation to this reference point, even ecologically-managed monocultures can be expected to exhibit an impoverish biota, as has been shown for different taxa (Fonseca et al. 2009a). The older ecologically-managed monocultures of *Araucaria angustifolia* (43–55 years old) are, in contrast to the beech monocultures, a good environment for the establishment of many canopy and understorey plant species. Young monocultures of exotic *Pinus* (30–37 years old) and *Eucalyptus* (8–30 years old), therefore, clearly provide fewer opportunities for additional biodiversity to be established. Along the land use gradient a decrease in plant species richness occurs from *Araucaria* forest (53 ± 3.5 [SE] species) and plantation of *Araucaria* (47.3 ± 3.8), to plantations of *Pinus* (29 ± 1.5) and *Eucalyptus* (26 ± 13.3) (Emer and Fonseca 2011).

In Germany, the unmanaged beech forests located in the national park are locally considered to be the best actual scenario in terms of conservation. They certainly do not reflect the state of a pristine beech forest, since these areas suffered an unknown impact of humans in the last 3000 years and some reports from the middle ages indicate sometimes heavy forest use by local farmers and nobles (Schulze et al. 2010). Despite that, the maximum age of trees and the amount of coarse woody debris are higher in unmanaged patches than in all different classes of managed beech forests. However, in temperate Central Europe a lack of disturbance in forests combined with the general dominance of beech leads to a closed canopy layer which in turn favours beech seedlings in the generally less well established understorey. Thus unmanaged beech forests almost represent a beech monoculture. There are indications that high densities of deer favour beech because other tree species suffer more from deer herbivory (Schulze et al. 2010). Species richness of herbs is low in unmanaged beech forests due to the closed beech canopy. In contrast, herb species richness is higher in managed than in unmanaged beech forests because of management related disturbances of the canopy and soil. In the Hainich region herb richness is in fact highest in pure spruce forests (S. Boch unpublished data).

Patterns of invertebrate abundances

Mean abundances were surprisingly similar among regions when standardized to 100 trap-days. More interesting, however, was the opposite patterns of abundance along the land use gradient among both regions. The negative effect of land use intensity on abundance of soil-dwelling invertebrates in the subtropics is consistent with the overall result for 13 different taxa found in the same experimental setup (Fonseca et al. 2009a). In this context, the replacement of *Araucaria* forest by ecologically-managed monocultures tends to produce an impoverished fauna. The causes behind such declines are under debate. One could expect, for instance, the abundance of litter-dwelling invertebrates to be related to the production of leaf litter, however, in the subtropical sites there is no difference in the yearly production of leaf litter between the four land use habitats (Bristot 2008). Nevertheless, since the diversity of associated woody plants in unmanaged *Araucaria* forest is greater than in the monocultures (Fonseca et al. 2009a), the quality of leaf litter varies among habitats, being richer in nutrients, specially N and P, in relation to the monocultures (Bristot 2008). In the temperate region the diversity of woody plants is significant higher in plantations of spruce than in managed and unmanaged beech forests (S. Boch unpublished data). This might explain the increased invertebrate abundances on spruce plantations. The higher structural and microclimatic heterogeneity in spruce plantations might additionally have favoured invertebrate abundances. Together, this suggests that bottom-up forces are organizing the litter-dwelling invertebrates in both regions (Price 2002).

Patterns of taxonomic richness and composition

Our finding that absolute and rarefied taxonomic richness was higher in the subtropical than in the temperate region is consistent with previous studies of the latitudinal gradient in biodiversity (Pianka 1966; Gaston 2000; Hillebrand 2004), although some failed to find this patterns, (e.g. Andrew and Hughes 2005) who studied the arthropod community structure across a latitudinal gradient in Australia. Thus, the pattern we found is itself not surprising, but highlights that, for litter-dwelling communities, the latitudinal diversity gradient is also valid for higher taxonomic resolution.

Taxonomic richness was not affected by land use intensity in both the subtropical and temperate region. This pattern is even clearer for the rarefied data. This suggests that higher taxa are resistant to local extinction even under the most extreme land uses considered in our study (i.e. younger plantations of *Eucalyptus* and plantations of spruce). For the temperate sites, which had their individuals fully identified to species, α -diversity also does not seem to respond to land use intensity (M. M. Gossner unpublished data). Due to shortage of local taxonomists, it was also not possible to identify all subtropical individuals to species which restricted the possibilities of analyzing community structure in more detail. However, rarefied species richness of flatworms and opiliones also did not respond to land use intensity (Fonseca et al. 2009b).

Subtropical and temperate sites differed in the overall taxonomic composition. Tropical sites had, among others, a higher relative abundance of grasshoppers, termites, cockroaches, ants and true bugs and lack of slugs. Both regions had several exclusive taxa, such as scorpions in subtropical sites and snakeflies in the temperate region. However, by performing a PCA after omitting the exclusive taxa, the separation between the tropical and temperate region still remains (data not shown). At subtropical sites Collembola and Coleoptera were the two most abundant taxa while Acarina and Collembola dominated the assemblages in the temperate regions. Studies in a tropical rainforest and tropical

countryside also found that Collembola and Coleoptera were the most abundant orders of litter-dwelling arthropods (Goehring et al. 2002; Medianero et al. 2007). Medianero et al. (2007) assumed that other studies reporting ants as most abundant taxon in pitfall traps might have been biased by not considering micro-arthropods, like Collembola or Acarina. Hence, the dominance of Collembola and Coleoptera in pitfall trap samples might therefore be a general pattern in tropical and subtropical forests. For temperate forests, the dominance of Coleoptera and Diptera seems to be widespread.

Guild abundance and structure

Despite the taxonomic differences, the number of individuals recorded for the different feeding guilds were surprisingly similar between subtropical and temperate sites, and hence there was also a close agreement in their relative fraction. The absence and lower numbers of some taxonomic groups seem to be compensated by the presence and higher abundance of other taxonomic groups of the same feeding guild. This suggests convergence of the functional structure of the litter-dwelling invertebrate communities among both climatic regions.

The response of the different feeding guilds to land use intensity exhibited opposite patterns in the two climatic regions. In the subtropical sites, the abundance of herbivores, parasites, predators, and omnivores (which probably are mainly predators due to the dominance of Coleoptera in the samples) were higher in the *Araucaria* forest and tended to decrease along land use gradient. In the temperate region, more intensively used sites tended to have higher abundance of most guilds. These results suggest that resource-driven productivity patterns can flow up the food chain, reaching primary producers, herbivores, omnivores, predators and parasites (Fonseca et al. 2005). The reasons for the relatively high abundance of detritivores in *Araucaria* plantations remain unclear.

Changing land use in forest systems certainly produces changes in biodiversity, but our study indicates that the effects of management may depend on the history of the particular forest system. Our results show that ecologically-managed plantations of dominant native tree species in both, a subtropical and a temperate site, lead to moderate effects on forest biodiversity. In the subtropics, the litter-dwelling invertebrate community is negatively affected by disturbance. However, the temperate data-set suggests that some degree of disturbance promotes biodiversity.

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