

Assemblage composition of ants (Hymenoptera: Formicidae) affected by tree diversity and density in native timber tree plantations on former tropical pasture

Judith RIEDEL, Silvia DORN & Karsten MODY



Abstract

Afforestation of degraded tropical pastures with native timber trees may enhance biological diversity and provide goods and services to local communities. We tested the hypothesis that afforestation schemes affect ant diversity differentially, depending on tree stand diversity. We quantified structure and composition of arboreal ant assemblages on the native timber tree *Tabebuia rosea* (Bignoniaceae) in experimental plantations on former pasture in Central America to assess the effects of (1) tree stand diversity in an afforestation system with *T. rosea* planted in a three species mixture or in monoculture and of (2) a combination of *T. rosea* with companion trees in a silvopastoral system, with *T. rosea* being surrounded by either *Guazuma ulmifolia* (Malvaceae) or *Gliricidia sepium* (Fabaceae).

We sampled 22 and 28 ant species in the pasture afforestation and in the silvopastoral system, respectively, with *Ectatomma ruidum* (ROGER, 1860), *Camponotus lindigi* MAYR, 1870, and *Solenopsis geminata* (FABRICIUS, 1804) being the dominant species. In the pasture afforestation system, the three species tree mixture surpassed the *Tabebuia rosea* monoculture in ant diversity, as expressed by species richness, ICE (incidence based estimator of species richness), and Simpson index. Branch sampling did not indicate any difference in ant density among the planting schemes, but activity at baits was significantly higher in the monoculture than in the mixture. In the silvopastoral system, companion trees supported ant diversity on the central *T. rosea* tree, as species richness and ant activity at baits were significantly higher on the central tree surrounded by companion trees than on solitary *T. rosea* trees. Furthermore, ICE of *T. rosea* trees accompanied by *Gliricidia sepium* was significantly higher than ICE of solitary trees. The highest species similarity was found for *T. rosea* trees surrounded by the different companion tree species, whereas ant assemblages of *T. rosea* trees in monoculture were most dissimilar to all other planting schemes. Our study demonstrates that while newly established plantations of native timber trees on former pasture might host moderately diverse ant assemblages, well-conceived diversification-afforestation schemes are promising for enhancement of ant diversity.

Key words: Ant diversity, arboreal ant communities, biodiversity conservation, insect-plant interactions, mixed-species timber plantations, Panama, smallholder forestry, silvopastoral systems, tree diversity.

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Introduction

Ecological restoration that reconciles conservation with agroforestry is a powerful approach to counteract negative environmental and socioeconomic effects of agricultural expansion and land degradation in the tropics (GARRITY 2004, LAMB & al. 2005, VANDERMEER & PERFECTO 2007). Trees within the farmland enhance the structural diversity and thereby provide resources and habitat for plant and animal species, increase landscape connectivity, and might serve as starting point for the re-establishment of woodland after the abandonment of land in the course of rural-urban migration (HARVEY & al. 2006, GRAU & AIDE 2008, DORROUGH & al. 2012). Regarding rural livelihoods, trees

on farms improve the value of the land and can increase farm productivity through the diversification of production and income (HALL & al. 2011b, MURGUEITIO & al. 2011, WETTERER 2011). Furthermore, if timber tree species are used, they can act as a savings account and provide additional income when needed (TRAGER 1991). Planting native trees instead of exotic tree species may enhance biological diversity (HARTLEY 2002, STEPHENS & WAGNER 2007, SMITH & al. 2013) and provide a broader range of valuable goods and services to local communities (FOLGARAIT & al. 1995, GAREN & al. 2011, HALL & al. 2011a).

Whereas classical timber plantation schemes are typically monocultures, more diversified schemes have been proposed, primarily for ecological reasons, however, with the potential for an economical benefit as well (HARTLEY 2002, BROCKERHOFF & al. 2008). In pasture afforestation systems characterized by high density plantings, it might be more advantageous to combine several tree species in mixtures than simply planting monocultures (HARTLEY 2002, ERSKINE & al. 2006, PIOTTO & al. 2010). Tree species mixtures can lead to higher growth performance compared to monocultures, provided compatible species and appropriate planting sites are chosen (FORRESTER & al. 2005, KELTY 2006, RIEDEL & al. 2013c). According to the associational resistance hypothesis, heterospecific neighbor trees may lower specialist herbivore loads depending on the identity and biology of the herbivore species, thereby limiting herbivory considerably (TAHVANAINEN & ROOT 1972, PLATH & al. 2012b). In afforestation systems characterized by low density timber planting, reconciliation of tree establishment with pasture use will allow continuous cattle ranching (DAGANG & NAIR 2003, WISHNIE & al. 2007), which is a vital part of agro-economy and culture in Latin America (WASSENAAR & al. 2007, FAO 2009). Such integrated systems, termed silvopastoral systems, may consist of single timber trees on pastures, or of central timber trees surrounded by companion trees (PLATH & al. 2011a, RIEDEL & al. 2013b). In both cases, the trees provide shade for livestock. Planting of companion trees may bring numerous added benefits as they protect timber tree seedlings from trampling and grazing, offer food supplement for livestock in the dry season (DAGANG & NAIR 2003, LOVE & al. 2009), and provide further species-specific goods and services (CAJAS-GIRON & SINCLAIR 2001). Based on experimental evidence, particularly promising native tree species are the timber species *Tabebuia rosea* due to its high survival and reliable growth under a wide range of biotic and abiotic conditions (VAN BREUGEL & al. 2011, RIEDEL & al. 2013c), as well as the multipurpose companion tree species *Guazuma ulmifolia* and the timber-growth supporting, nitrogen-fixing *Gliricidia sepium* (see GRAHAM & VANCE 2003, WISHNIE & al. 2007, RIEDEL & al. 2013b).

Yet, for native tree plantations on former pasture it remains largely unclear, which level of faunal diversity they can sustain. Vegetation structure and diversity of grassland benefitted from such afforestations, and floristic biodiversity was increased (HALL & al. 2012, SOUZA & al. 2013). It is also unknown whether mixed stands of native tropical trees in pasture afforestations harbor higher levels of faunal diversity than respective monocultures.

Herbivory was found to be often but not always lower in mixed tree stands of various temperate or tropical systems (JACTEL & al. 2005, VEHVILAINEN & al. 2007, LETOURNEAU & al. 2011, PLATH & al. 2011b, 2012b), and measures of beetle diversity were not necessarily higher in mixed stands than in monocultures of native tropical timber trees (PLATH & al. 2012a). For silvopastoral systems, to date no evidence exists whether companion planting of heterospecific trees around a central timber tree holds potential to increase faunal diversity.

In the present study, we tested the hypothesis that ant diversity in newly established planting systems is affected by the planting scheme used for afforestation. Although the enemies hypothesis (ROOT 1973) predicts that diversity of

herbivores and their antagonists increases with plant diversity, in tropical tree ecosystems effects of tree species composition and stand characteristics might be more relevant for diversity than tree stand diversity per se (VEHVILAINEN & al. 2008, PLATH & al. 2012a). Furthermore, temporal variation in the composition of arthropod assemblages might be high (GORDON & al. 2009, TANAKA & al. 2010, WARDHAUGH & al. 2012), and effects of stand diversity might change over time (DELAGRANGE & al. 2008, RIEDEL & al. 2013c).

To study effects of planting schemes on faunal diversity, we selected ants as focus group as they are an essential component of tropical diversity in natural and disturbed ecosystems and extremely important in structuring arthropod communities (HÖLLDOBLER & WILSON 1990, MODY & LINSÉNMAIR 2004, CRIST 2009). Ants are among the major predators in tropical forestry systems (FLOREN & al. 2002, ROSUMEK & al. 2009) and may act as natural bio-control agents that benefit trees through reducing insect herbivory (PHILPOTT & ARMBRECHT 2006, SORVARI 2009, RIEDEL & al. 2013a). Furthermore, ants often reflect the degree of habitat disturbance and therefore comprise valuable indicators of ecosystem conditions (ANDERSEN & MAJER 2004, HOFFMANN 2010, ELLISON 2012).

In this study we assessed the effect of different planting schemes on ants in two different planting systems, (1) a pasture afforestation system with high density planting of the native timber tree *Tabebuia rosea* in monoculture or in a three species mixture, and (2) a silvopastoral system with low density planting of this native timber tree, growing solitary or associated with two different species of multipurpose companion trees, *Gliricidia sepium* and *Guazuma ulmifolia*. The specific objectives were to (I) record ant diversity, (II) compare ant diversity among different planting schemes of a pasture afforestation system and a silvopastoral system, and (III) quantify temporal changes in ant diversity with progressing season and tree age.

Methods

Study site and species: The study was conducted from July 2009 (year 1) to November 2011 (year 3) in a native tree plantation in Sardinilla, Central Panama (9° 19' 30" N, 79° 38' 00" W, elevation 70 m a.s.l.), about 40 km north of Panama City and 30 km northeast of Barro Colorado Island. The climate at the study site is semi-humid tropical with a mean annual temperature of 25.2°C, a mean annual precipitation of 2289 mm and a dry season from January to April (134 ± 19 days) (WOLF & al. 2011). The semi-deciduous lowland rainforest previously covering the study site was logged in 1952 / 53, and after two years of agricultural use the site was converted into pasture and grazed by cattle for almost 50 years (POTVIN & al. 2004), leaving only remnant trees but no native forests in the landscape surrounding the study site.

The selected focal plant species *Tabebuia rosea* BERTOL. (Bignoniaceae) is a native timber tree of commercial value with good growth potential across different environmental conditions, and it has a high suitability for pasture afforestation (PLATH & al. 2011a, b, and references therein). Its natural distribution ranges from Southern Mexico to Venezuela, its habitats comprise wet-, moist-, and dry forests, and it is cultivated in plantations throughout the tropics (GENTRY 1973, WISHNIE & al. 2007). This deciduous tree



Fig. 1: The branch elector traps used to record the abundance of arboreal ants. The traps consisted of a ring of black duct tape, a plastic funnel, and a container. The duct tape was fitted tightly around a branch and treated with FLUON to create a slippery surface. The funnel was hung beneath, leading into a plastic container filled with saturated NaCl solution as preservation liquid. The container featured an overflow hole that was covered with gauze.

species, which attains a height of 25 - 30 m, sheds its leaves during the dry season and flushes new leaves in the early rainy season (GENTRY 1970). It bears scale-like extrafloral nectaries that secrete a modest amount of nectar on young stems and the surfaces of its palmate, five-foliolate leaves (DIAZ-CASTELAZO & al. 2005).

Planting design: Two planting systems were established on former pasture in August 2006, i.e., three years before the current study began: a pasture afforestation system and a silvopastoral system (PLATH & al. 2011a, b).

Within the pasture afforestation system, *Tabebuia rosea* was planted either in monoculture or in a three species mixture together with the native timber trees *Anacardium excelsum* (BETERO & BLAB. EX KUNTH) SKEELS (Anacardiaceae) and *Cedrela odorata* L. (Meliaceae). Trees were established at high densities at a spacing of 2 m in stands of 36 trees using a standardized six by six Latin square design. The two stand types were replicated five times at different locations across the study site (PLATH & al. 2011b).

Within the silvopastoral system, *Tabebuia rosea* was planted at low densities at a spacing of 9 m in three different planting schemes: (1) *T. rosea* trees surrounded by the legume companion species *Gliricidia sepium* (JACQ.) KUNTH EX WALP. (Fabaceae); TGli), (2) *T. rosea* trees surrounded by the companion species *Guazuma ulmifolia* (LAM. (Malvaceae); TGua), and (3) solitary *T. rosea* trees

(TSol). In the first two planting schemes, five conspecific companion trees were planted circularly around the central timber tree at a distance of 1.5 m. The three planting schemes with eight *T. rosea* individuals each were randomly arranged within a coherent plot. This plot was replicated three times at different locations across the study site, resulting in a total of 24 timber tree individuals per planting scheme (PLATH & al. 2011a). In both systems, local site conditions (including soil moisture, soil pH, soil nitrogen content, and collateral vegetation) varied notably across and within plots (PLATH & al. 2011a, b).

Assessment of ant assemblages: Different sampling methods were used to assess ant assemblage composition (GOTELLI & al. 2011). Ants were sampled by a combination of branch beating, branch traps, as well as sugar and nitrogen baits. Furthermore, we recorded the nest density of two dominant ant species, *Ectatomma ruidum* (ROGER, 1860) (Ectatomminae) and *Camponotus lindigi* MAYR, 1870 (Formicinae) (RIEDEL & al. 2013a). In the pasture afforestation system, ants were sampled from 6 randomly selected *Tabebuia rosea* trees per tree stand, resulting in a total of 60 sampled trees, 30 trees in mixed stands and 30 trees in monoculture stands. In the silvopastoral system, ants were sampled from all *T. rosea* trees that had survived the establishment phase, i.e., 24 TGua, 22 TGli, and 23 TSol trees. Ants were determined to genus and morpho-species after HÖLLDOBLER & WILSON (1990), BOLTON (1994), and

FERNÁNDEZ (2003), and taxonomic experts (see acknowledgements) were consulted for the final identification of species and confirmation of morpho-species (in the following termed "species", but see Tab. 1 for details).

Abundance of arboreal ants recorded from branches of *Tabebuia rosea*: Ants were sampled from the tree crowns of the study trees at four periods in year 1 (09 - 22 July, 19 August - 1 September, 28 September - 2 October, 27 - 30 October) and at two periods in year 2 (24 - 27 August, 20 - 22 September) at day and night with a beating tray. The tray (0.5 m × 0.5 m) was positioned directly below the sampled branch, which was then shaken for approximately eight seconds. All ants in the tray were collected in an ethanol containing plastic container mounted to the bottom of the tray. Ant numbers of each branch were quantified as ant density by standardizing to the number of sampled leaves.

In addition to beating tray sampling, we recorded the abundance of arboreal ants by branch elector traps, which consisted of a ring of black duct tape, fitted tightly around a branch, a plastic funnel, and a container (KOPONEN 2004, STUNTZ & al. 1999). The duct tape was treated with FLUON (polytetrafluorethylene, PTFE) to create a slippery surface. The funnel was hung beneath, leading into a plastic container filled with saturated NaCl solution as preservation liquid (Fig. 1). The container had an overflow hole below the lid, which was covered with gauze. Traps were installed end of July of year 2 and left in the crowns of the study trees for 14 days.

Ant activity at baits: To estimate the potential ant activity per study tree, we quantified the abundance of each ant species by using baits mounted to the tree trunks. In year 1, we placed a set of two types of baits in the tree crowns of the study *Tabebuia rosea* trees. Baits consisted of either 4 g of tuna ("nitrogen bait") or a piece of cotton soaked in 4 ml saturated sucrose solution ("sugar bait"), and they were put on a wooden plate with an area of 10 cm², which was attached horizontally to the branch using a thin wire. The maximum distance between the two baits was 20 cm. We observed the baits during the day, between 7:30 h and 15:00 h, 30 min, 1 h, 2 h, and 3 h after bait placement and recorded number of ant species and individuals present on the wooden plate. Recordings were conducted for one week at the end of July in year 1. As recruitment of ants to the baits was slow, we used the recording of ant individual numbers 2 h after mounting the bait for statistical analysis and as the standard recording time in subsequent assessments.

Based on the experience of year 1, we adjusted the method and quantified ant abundance at baits in year 2 by using sugar baits that consisted of cut-open Eppendorf tubes (2 ml) filled with saturated sucrose solution and cotton (BLÜTHGEN & al. 2006, RIEDEL & al. 2013a). The cotton protruded as a wick to the tree trunk and made the solution available to ants. One bait per tree was attached to the trunk at 1.60 m height. We counted all ant individuals within a radius of 5 cm around each bait in four sampling events (4 August, 31 August - 1 September, 17 / 18 September, 10 November), consisting of a night and a day assessment. To ensure relatively consistent climatic diel conditions and to consider periods of high ant activity, ant counts were conducted between 20:00 h and 22:00 h for the night assessments and between 07:00 h and 10:30 h for the day as-

sessments. Ant activity was re-assessed in year 3 (31 October - 3 November) by conducting one sampling each at day and night, using the same method as in year 2.

Occasionally, individual numbers of *Solenopsis geminata* (FABRICIUS, 1804; Myrmicinae) were exceedingly high. Counting was then discontinued at 50 individuals, and abundance was recorded as 50 individuals, taking into account an underestimation of total abundance of this species. For each ant species not readily identifiable in the field, one to three reference specimens (depending on the number of ant individuals at the bait) were collected per bait and stored in 75% ethanol for later identification. In case a single ant specimen escaped without prior identification of the genus, it was listed as "unidentified species".

Nest density of *Ectatomma ruidum* and *Camponotus lindigi*: Nest density of two dominant ant species, *Ectatomma ruidum* and *Camponotus lindigi*, was recorded in the pasture afforestation system and in the silvopastoral system by attracting ants with sugar baits as described above. Baits were directly attached to the trunks of *Tabebuia rosea* 40 cm above the ground. In order to representatively assess nest density, ant workers departing from the baits were followed to their nests within a radius of 60 cm around the examined *T. rosea* tree, yielding a standardized "observation circle" of approximately 1 m². Two hours after mounting the bait, each observation circle was then monitored for 20 minutes and the number of nest entrances in the observation circle was recorded. As the typical structure of the ground nests of *E. ruidum* has been described as having only one entrance (LEVINGS & FRANKS 1982), each nest entrance was counted as one colony, unless the distance between entrances was less than 10 cm. Since *Camponotus lindigi* was observed to nest in hollow twigs (J. Riedel, unpubl.), the number of nests was observed directly. In pasture afforestation plots, nests were recorded around the stems of 12 randomly selected *T. rosea* trees. In silvopastoral plots, nests were recorded around each *T. rosea* tree and additionally in a 10 m × 10 m area in the open pasture, where baits were placed on wooden sticks, concordantly with the setup in the pasture afforestation system. Of each colony one to four reference specimens were collected and preserved in 75% ethanol.

Data analysis: To describe ant assemblage composition, we determined ant incidence (I), ant abundance (N), species richness (S), the incidence-based coverage estimator of species richness (ICE) and the inverse Simpson index (Si) for each tree, and we compared the similarities of ant assemblages among planting schemes and individual trees with the classical Jaccard similarity index (CHAO & al. 2000, MAGURRAN 2004) using the software EstimateS Mac 9.0.0. (COLWELL 2009). Ant species richness and abundance were calculated as the cumulated number of species / individuals recorded at day and night at each tree. Ant incidence was calculated as the proportion of assessments in which a single species was present on each tree in relation to the total number of assessments. ICE and Simpson index were calculated for ants recorded with branch samplings and baits using only identified individuals. ICE and Simpson index were not calculated for ants sampled with branch traps, as this sampling method comprised only one recording. ICE, Simpson index, and species richness were compared among planting schemes by linear mixed effect models, considering planting schemes as fixed fac-

Tab. 1: Diversity and incidence of ants collected from *Tabebuia rosea* using branch sampling, branch traps, and recordings at baits on tree trunks. Incidence values are shown and represent the proportion of assessments in which a single species was present on each tree in relation to the total number of assessments. Total individual numbers are shown additionally in brackets. Diversity indices characterizing ant assemblages comprise species richness, the incidence-based coverage estimator of species richness (ICE), and the inverse Simpson index calculated for each tree (mean \pm SE) (CHAO & al. 2000, MAGURRAN 2004). Incidence values and diversity measures are based on identified ant individuals, and except for species richness, were not calculated for ants sampled with branch traps, as this sampling consisted of only one assessment per tree. n. a. = not applicable. *Camponotus atriceps* was formerly known as *C. abdominalis*.

Taxon	Pasture afforestation system			Silvopastoral system		
	Branch samples	Branch traps	Baits	Branch samples	Branch traps	Baits
Ectatomminae						
<i>Ectatomma ruidum</i>	0.178 (112)	0.517 (100)	0.406 (1377)	0.150 (156)	0.257 (66)	0.242 (742)
Formicinae						
<i>Brachymyrmex</i> sp. 1	0.011 (4)	0	0	0.010 (4)	0	0
<i>Camponotus atriceps</i>	0	0.033 (5)	0.047 (48)	0.017 (8)	0.029 (2)	0.106 (227)
<i>Camponotus lindigi</i>	0.186 (90)	0.117 (12)	0.147 (192)	0.304 (287)	0.174 (19)	0.254 (391)
<i>Camponotus</i> sp. 2	0.108 (60)	0.050 (3)	0.005 (45)	0.053 (35)	0.058 (10)	0.034 (33)
<i>Camponotus</i> sp. 3	0.028 (12)	0	0.003 (1)	0.012 (5)	0	0.005 (2)
<i>Camponotus sanctaefidei</i>	0	0	0	0.002 (1)	0	0
<i>Camponotus</i> sp. 5	0	0	0	0	0	0.002 (10)
<i>Camponotus</i> sp.	0	0	(5)	0	0	(10)
<i>Nylanderia</i> sp. 1	0	0	0.008 (15)	0.007 (3)	0	0.005 (5)
Myrmicinae						
<i>Crematogaster</i> sp. 1	0.006 (2)	0	0.003 (6)	0.024 (23)	0	0.007 (27)
<i>Crematogaster</i> sp. 2	0.003 (1)	0.017 (1)	0	0.002 (2)	0	0.002 (30)
<i>Crematogaster</i> sp.	0	0	(8)	0	0	(112)
<i>Cyphomyrmex rimosus</i>	0.003 (1)	0.017 (5)	0	0	0.014 (1)	0
<i>Monomorium floricola</i>	0	0	0	0.007 (3)	0	0
<i>Monomorium</i> sp. 2	0	0	0	0.002 (1)	0	0
<i>Pheidole rugiceps</i>	0.003 (1)	0	0	0.002 (1)	0.029 (2)	0
<i>Pheidole ruida</i>	0	0	0	0.002 (1)	0	0
<i>Pheidole</i> sp.	0	(2)	(66)	0	(1)	(25)
<i>Solenopsis geminata</i>	0.006 (2)	0.050 (7)	0.047 (764)	0.036 (25)	0.072 (10)	0.116 (1982)
<i>Solenopsis</i> sp. 1	0.006 (2)	0	0	0.007 (3)	0	0.002 (5)
<i>Strumigenys marginiventris</i>	0.003 (1)	0	0	0	0	0
<i>Wasmannia auropunctata</i>	0	0	0	0	0.014 (1)	0.002 (2)
Dolichoderinae						
<i>Forelius damiani</i>	0.011 (4)	0	0.003 (4)	0.017 (12)	0	0.012 (22)
<i>Linepithema</i> sp. 1	0	0	0.006 (23)	0	0	0
<i>Azteca</i> sp. 2	0.003 (1)	0	0	0	0	0
<i>Dolichoderus bispinosus</i>	0	0	0	0.012 (8)	0.014 (1)	0.007 (39)
<i>Tapinoma melanocephalum</i>	0	0	0	0.002 (1)	0	0
Ecitoninae						
<i>Eciton burchellii</i>	0	0.033 (2)	0	0	0.014 (1)	0
Ponerinae						
<i>Hypoponera</i> sp. 1	0.003 (1)	0	0	0	0	0
Proceratinae						
<i>Discothyrea humilis</i>	0	0	0	0.002 (1)	0	0
Pseudomyrmecinae						
<i>Pseudomyrmex gracilis</i>	0.019 (7)	0.117 (10)	0.011 (4)	0.053 (24)	0.101 (7)	0.019 (12)
<i>Pseudomyrmex oculatus</i>	0	0.017 (1)	0	0.002 (1)	0	0
<i>Pseudomyrmex pallidus</i>	0.003 (1)	0.050 (3)	0.006 (4)	0.022 (11)	0.014 (1)	0.002 (2)
Unidentified	(10)	(2)	(10)	(14)	(0)	(75)
Species total	17	11	12	23	12	16
Individuals total	312	149	2572	630	123	3753
Species richness	2.1 \pm 0.1	1.2 \pm 0.2	2.1 \pm 0.1	2.8 \pm 0.2	0.8 \pm 0.1	2.5 \pm 0.1
ICE	3.6 \pm 0.4	n. a.	3.7 \pm 0.4	6.2 \pm 0.8	n. a.	4.3 \pm 0.4
Simpson index	1.7 \pm 0.1	n. a.	1.5 \pm 0.1	2.0 \pm 0.1	n. a.	1.6 \pm 0.1

tors and plots as random factors (PINHEIRO & BATES 2000). Ant assemblage similarities between individual trees, nest density, and ant incidence at baits, branch traps, and in branch samplings were compared among planting schemes with Kruskal-Wallis tests (silvopastoral system) and U-tests (pasture afforestation system). In the silvopastoral system, nest densities of each planting scheme were compared to nest densities in the open pasture by U-tests. Significant differences in Kruskal-Wallis tests were followed by U-tests as post-hoc tests. To correct for multiple testing, false discovery rate correction was applied (VERHOEVEN & al. 2005). Total ant incidence as well as incidence of *Ectatomma ruidum* and *Camponotus lindigi* at baits were compared among sugar baits and nitrogen baits by paired Wilcoxon tests. Nest densities of *E. ruidum* and *C. lindigi* were related to each other by a classical interspecific association analysis, using χ^2 -tests (LUDWIG & REYNOLDS 1988). To assess temporal changes in ant assemblage composition, we used Friedman's ANOVA with Wilcoxon tests as post-hoc procedure (significance values adjusted after false discovery rate correction). Linear mixed effect models were performed using R 2.14.0 (2011, The R Foundation for Statistical Computing). All other statistical analyses were performed using the software SPSS 20.0 for Mac OS X (2010 SPSS, Chicago, IL, USA).

Results

Ant diversity on *Tabebuia rosea* planted on former pasture: In the pasture afforestation system we recorded 22 ant species overall. In the tree crowns of *T. rosea* we collected 312 ant individuals belonging to 17 species by branch sampling in year 1 and year 2, and 149 ant individuals belonging to 11 species with branch traps in year 2 (Tab. 1). The ant assemblage on the branches of *T. rosea* was dominated by two species, *Ectatomma ruidum* and *Camponotus lindigi*, which had the highest incidence values and together accounted for 67% (branch samples) and 75% (branch traps) of the recorded individuals (Tab. 1). At baits mounted to trunks of *T. rosea*, we observed a total of 2572 ant individuals, which belonged to 12 species (Tab. 1). The ant assemblage recorded by baiting was dominated by three species: *E. ruidum* (54%), *C. lindigi* (7%), and *Solenopsis geminata* (30%). Although *S. geminata* accounted for almost one third of the individuals, it showed comparably low incidence, meaning that it was observed at the baits at few times but each time with high individual numbers (Tab. 1).

In the silvopastoral system we recorded 28 ant species in total: we collected 630 ant individuals belonging to 23 species by branch sampling, 123 ant individuals belonging to 12 species with branch traps, and recorded 3753 individuals belonging to 16 species at baits (Tab. 1). Similar to the pasture afforestation system, the ant assemblage on the branches of *Tabebuia rosea* was dominated by *Ectatomma ruidum* and *Camponotus lindigi* (Tab. 1). As in the pasture afforestation system, the two species were represented differently by the two sampling methods: While *E. ruidum* had the highest incidence in branch traps, *C. lindigi* had the highest incidence in branch samplings. Although *S. geminata* was the most abundant species at baits, its incidence was lower than that of *E. ruidum* and *C. lindigi* (Tab. 1). Overall, ant diversity recorded by the different sampling methods was low but higher in the silvopastoral system

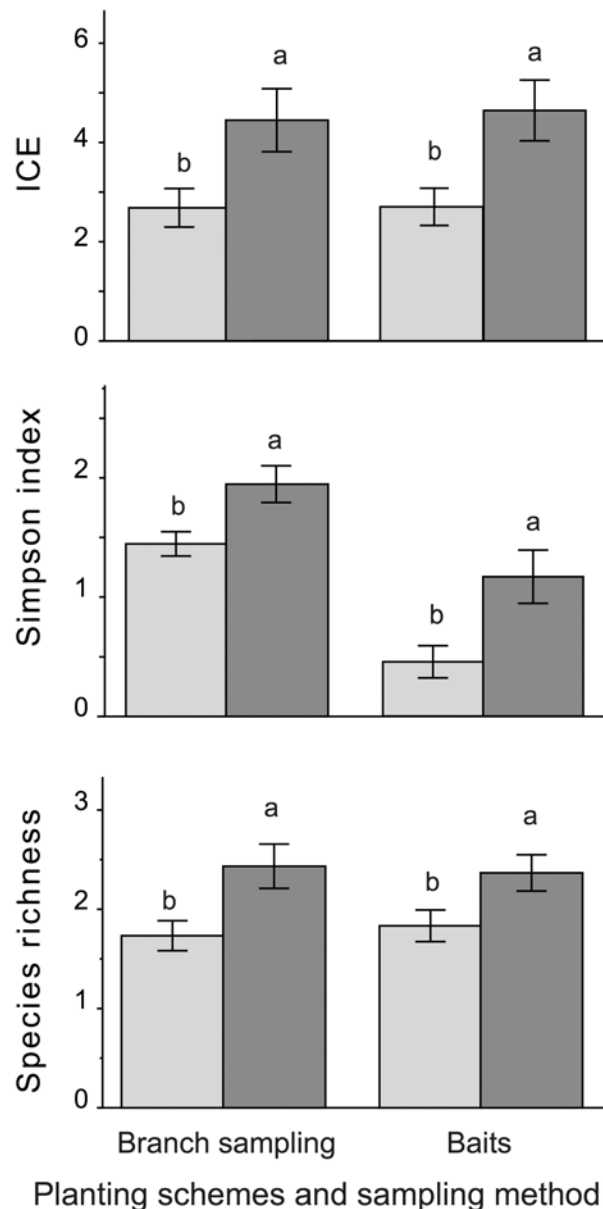


Fig. 2: Effects of planting schemes on ant assemblage composition of the native timber tree *Tabebuia rosea* in a pasture afforestation system. Planting schemes represent monocultures of *T. rosea* (light grey) and three species mixtures of *T. rosea*, *Anacardium excelsum*, and *Cedrela odorata* (medium grey). Shown are means \pm SE of assemblage measures assessed by branch sampling and with baits. ICE = incidence based coverage estimator of species richness. Different letters above bars indicate significant differences (linear mixed effect model, $P < 0.05$).

than in the pasture afforestation system (Tab. 1). The comparably highest values were observed in the silvopastoral system by branch sampling with an ant species richness of 2.8 ± 0.2 (mean \pm SE) per tree, an incidence-based coverage estimator of species richness (ICE) of 6.2 ± 0.8 , and a Simpson index of 2.0 ± 0.1 (Tab. 1). *Linepithema* sp. (Dolichoderinae) was found in the pasture afforestation system but not in the silvopastoral system. Contrastingly, the little fire ant *Wasmannia auropunctata* (ROGER, 1863; Myrmicinae) and *Dolichoderus bispinosus* (OLIVIER,

Tab. 2: Effects of planting schemes on ant assemblage composition of the timber tree *Tabebuia rosea*. Ants were sampled by branch sampling, at sugar baits attached to the tree trunk, and by branch traps. Ant assemblages were characterized by ant incidence (I), species richness (S), the incidence-based coverage estimator of species richness (ICE), and the inverse Simpson index (Si) (CHAO & al. 2000, MAGURRAN 2004) calculated per tree individual. Planting schemes in the pasture afforestation system represent monocultures of *T. rosea* (MON) and three species mixtures of *T. rosea*, *Anacardium excelsum*, and *Cedrela odorata* (MIX). Planting schemes in the silvopastoral system represent *T. rosea* individuals growing surrounded by *Gliricidia sepium* (TGli), surrounded by *Guazuma ulmifolia* (TGua), or solitarily (TSol). Significant differences are highlighted in bold. Statistical analysis was done with linear mixed effects models where possible. Remaining variables (test statistics in italics) were tested with U-tests or KW-tests. Significant KW-tests were followed by U-tests as post-hoc tests, to which false discovery rate correction was applied (VERHOEVEN & al. 2005).

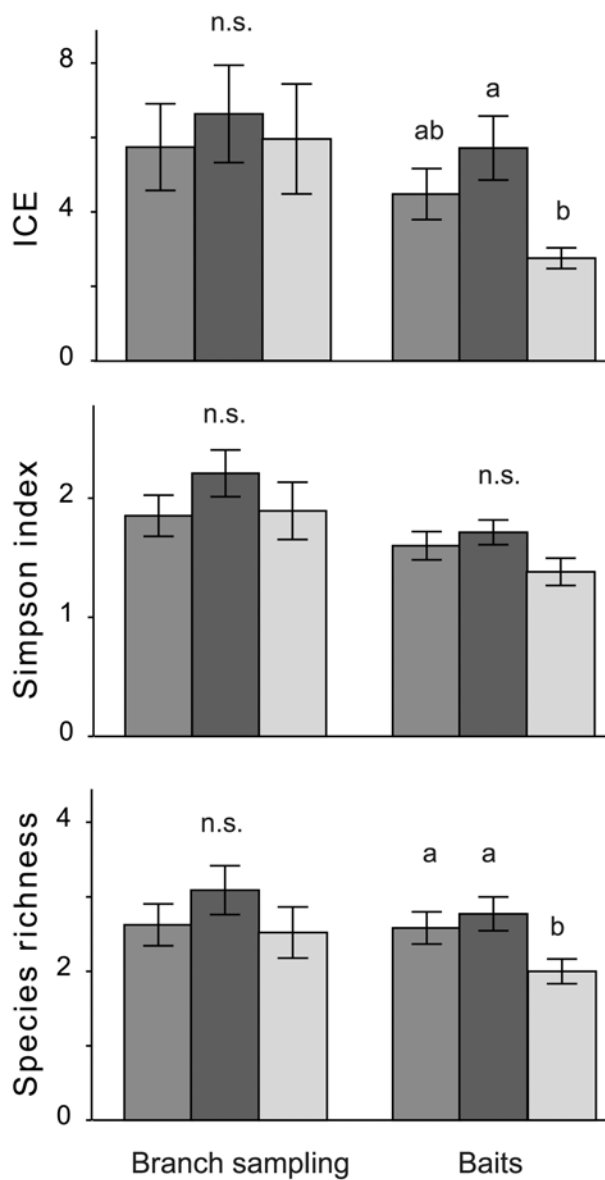
Planting system	Sampling method	Variable	numDF	denDF	Test Statistic	P
Pasture afforestation	Branch sampling	I			<i>431.0</i>	<i>0.779</i>
		S	1	54	6.74	0.012 (MIX^a > MON^b)
		ICE	1	54	5.62	0.021 (MIX^a > MON^b)
		Si	1	54	7.34	0.009 (MIX^a > MON^b)
	Baits	I			<i>410.5</i>	<i>0.544</i>
		S	1	54	4.84	0.032 (MIX^a > MON^b)
		ICE	1	54	7.31	0.009 (MIX^a > MON^b)
		Si	1	54	7.42	0.009 (MIX^a > MON^b)
	Branch traps	I			<i>400.5</i>	<i>0.421</i>
		S			<i>405.5</i>	<i>0.470</i>
Silvopastoral	Branch sampling	I			6.93	0.031 (TGua^a, TGli^{ab}, TSol^b)
		S	2	64	1.40	0.255
		ICE	2	64	0.22	0.805
		Si	2	64	1.33	0.273
	Baits	I			<i>2.97</i>	<i>0.226</i>
		S	2	64	3.82	0.027 (TGli^a, TGua^a > TSol^b)
		ICE	2	64	5.14	0.008 (TGli^a, TGua^{ab}, TSol^b)
		Si	2	64	2.25	0.114
	Branch traps	I			<i>2.53</i>	<i>0.282</i>
		S	2	64	0.69	0.503

1792; Dolichoderinae) were found only in the silvopastoral system. *Eciton burckellii* (WESTWOOD, 1842; Ecitoninae) was recorded incidentally in both systems with the continuously exposed branch traps. We did not record leaf cutter ants (*Atta* sp. (Myrmicinae)) on *T. rosea*, although we observed them in the vicinity of the study site (J. Riedel & K. Mody, unpubl.).

Effects of tree planting schemes on ant assemblages of *Tabebuia rosea*: In the pasture afforestation system, comparisons of diversity measures revealed significant effects of planting schemes on the ant assemblages of *T. rosea* (Fig. 2). In the branch samplings, species richness, ICE, and Simpson index were significantly higher in the three species (tree) mixture than in the monocultures of *T. rosea*, whereas ant incidence did not differ (Tab. 2). At baits, the tree mixture was again significantly higher than monocultures of *T. rosea* regarding species richness, ICE, and Simpson index (Tab. 2). In branch traps, species richness and ant incidence were not significantly different between planting schemes (Tab. 2). Considering the two bait types deployed in year one, total ant incidence was low at both bait types (sugar: 0, 0, 1 (quartiles), nitrogen: 0, 0, 1) and did not differ significantly ($Z = -0.928$, $P = 0.353$). Concordantly, we found no significant differences among sugar and nitrogen baits regarding incidence of the individual species *Ectatomma ruidum* ($Z = -0.832$, $P = 0.405$) and *C. lindigi* ($Z = -0.277$, $P = 0.782$).

In the silvopastoral system, the presence of companion tree species had significant effects on the ant assemblages of the central *Tabebuia rosea* trees (Fig. 3). At baits, species richness was significantly higher on *T. rosea* trees surrounded by *Gliricidia sepium* (TGli) or *Guazuma ulmifolia* (TGua) than on solitary trees (TSol; Tab. 2). The ICE of TGli trees was significantly higher than the ICE of TSol trees, and the Simpson index was higher on TGli and TGua trees than on TSol trees, although this last comparison was not significantly different (Tab. 2). In branch samplings ant incidence was significantly higher on TGua trees than on TSol trees. In branch traps, diversity measures were not significantly affected by planting schemes (Tab. 2). Considering bait types, we found a significantly higher total ant incidence at sugar baits than at nitrogen baits ($Z = -1.976$, $P = 0.048$). Concordantly, incidence of *Ectatomma ruidum* was significantly higher at sugar than at nitrogen baits ($Z = -2.333$, $P = 0.020$). Incidence of *Camponotus lindigi* did not differ between the two bait types ($Z = -0.655$, $P = 0.513$).

Temporal variation in ant assemblage composition: Temporal variation among recordings was high in branch samplings and at baits both in the pasture afforestation system and in the silvopastoral system (Tab. 3). In the pasture afforestation system, species richness of branch samplings did not differ significantly among recordings but ant density was significantly higher in the first record-



Planting schemes and sampling method

Fig. 3: Effects of planting schemes on ant assemblage composition of the native timber tree *Tabebuia rosea* in a silvopastoral system on former pasture. Planting schemes include *T. rosea* trees surrounded by *Guazuma ulmifolia* (medium grey), surrounded by *Gliricidia sepium* (dark grey), or growing solitarily (light grey). Shown are means \pm SE of assemblage measures assessed by branch sampling and with baits. ICE = incidence based coverage estimator of species richness. Different letters above bars indicate significant differences (linear mixed effect model, $P < 0.05$).

ing in June of year 1 (1.1) than in the other samplings (Tab. 3). Contrastingly, at baits species richness and ant activity were significantly higher in later recordings of year 2 and in year 3 than in year 1 and in the first recording of year 2, at the beginning of August (2.1; Tab. 3). In the silvopastoral system, species richness and ant density in branch samplings were significantly higher in the first recordings of year 1 (July, 1.1) and 2 (August, 2.1) than in almost all other recordings, particularly the third record-

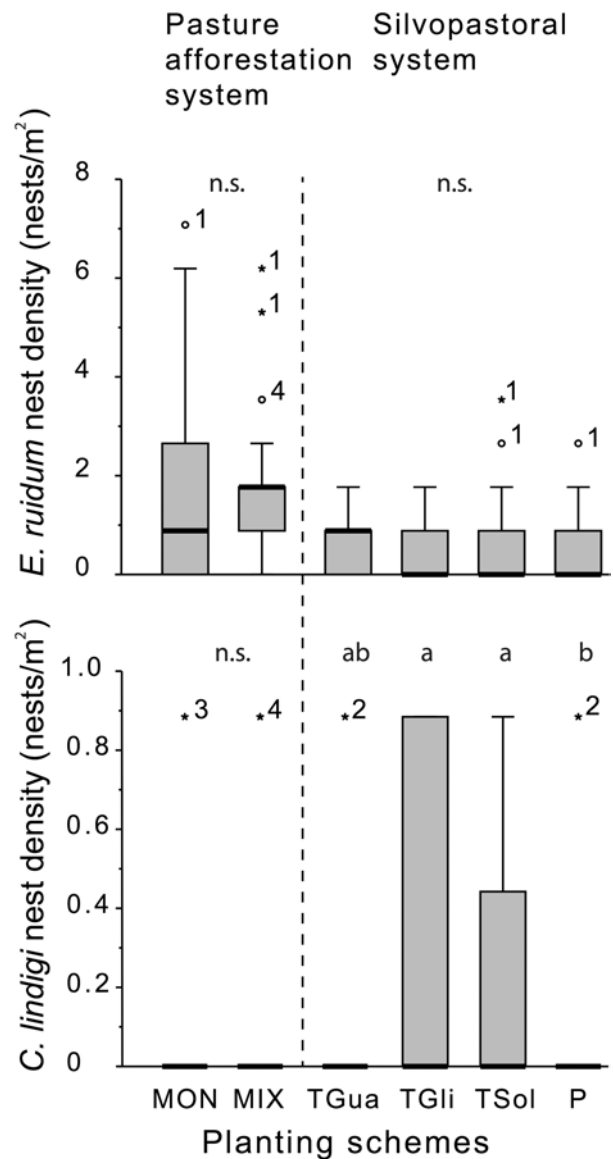


Fig. 4: Nest density of *Ectatomma ruidum* and *Camponotus lindigi* in different planting schemes (median, interquartile range), outliers (circles), and extremes (asterisks). In the pasture afforestation system, two planting schemes were established: monocultures of *Tabebuia rosea* (MON) and three species mixtures of *T. rosea*, *Anacardium excelsum*, and *Cedrela odorata* (MIX). In the silvopastoral system, planting schemes included *T. rosea* trees surrounded by *Guazuma ulmifolia* (TGua), surrounded by *Gliricidia sepium* (TGli), or growing solitarily (TSol). In the silvopastoral system nest density was furthermore recorded in the open pasture (P). Numbers next to outliers and extremes represent the number of cases. Different letters above bars indicate significant differences (U-test or KW-test, $P < 0.05$).

ing of year 1, end of August – September, 1.3; Tab. 3). At baits, species richness and ant activity were significantly higher in year 3 than in the first year (July, 1) and the first recording of year 2 (beginning of August, 2.1; Tab. 3).

Similarity of ant assemblages among planting schemes and individual trees: Analysis of species similarity indicated that species composition of ant assemblages on

Tab. 3: Temporal comparisons of ant assemblage composition of *Tabebuia rosea* (mean rank and non-parametric statistics). Ants were sampled by branch sampling and at baits attached to the tree trunk. Comparisons were done by comparing ant density (D; branch samplings), ant abundance (N; baits) and species richness (R) among different recordings, separately for the different sampling methods and the two planting systems, pasture afforestation system (PA) and silvopastoral system (SP). Recordings refer to study year (first digit) and sampling event within the year (second digit). Significant differences are highlighted in bold. Statistical analysis was done by Friedman's ANOVA with Wilcoxon tests as post-hoc procedure (significance values adjusted after false discovery rate correction).

Sampling method	Planting system	Variable	Recording						Statistics
			1.1	1.2	1.3	1.4	2.1	2.2	
Branch sampling	PA	D	4.23	3.18	3.22	3.54	3.66	3.17	$\chi^2_5 = 17.0$; $P = 0.004$ (1.1 ^a , 2.1 ^{ab} , 1.4 ^{ab} , 1.3 ^b , 1.2 ^b , 2.2 ^b)
		R	3.79	3.44	3.44	3.44	3.64	3.24	$\chi^2_5 = 4.6$; $P = 0.473$
	SP	D	4.21	3.25	2.93	3.18	4.16	3.26	$\chi^2_5 = 31.4$; $P < 0.001$ (1.1 ^a , 2.1 ^a > 2.2 ^b , 1.2 ^b , 1.4 ^b , 1.3 ^b)
		R	3.83	3.38	3.00	3.29	4.26	3.24	$\chi^2_5 = 29.1$; $P < 0.001$ (2.1 ^a , 1.1 ^{ab} , 1.2 ^{bc} , 1.4 ^{bc} , 2.2 ^c , 1.3 ^c)
Baits	PA	N	1	2.1	2.2	2.3	2.4	3	$\chi^2_5 = 47.8$; $P < 0.001$ (3 ^a , 2.4 ^a , 2.3 ^a , 2.2 ^a > 1 ^b , 2.1 ^b)
		R	3.20	2.67	3.78	3.87	3.97	3.53	$\chi^2_5 = 35.4$; $P < 0.001$ (2.4 ^a , 2.3 ^a , 2.2 ^a , 3 ^b , 1 ^{bc} , 2.1 ^c)
	SP	N	3.25	2.82	4.02	3.33	3.07	4.51	$\chi^2_5 = 43.9$; $P < 0.001$ (3 ^a , 2.2 ^{ab} , 2.3 ^{bc} , 2.4 ^c , 1 ^c , 2.1 ^c)
		R	3.36	2.81	3.75	3.54	3.42	4.12	$\chi^2_5 = 69.0$; $P < 0.001$ (3 ^a , 2.2 ^{ab} , 2.3 ^{ab} , 2.4 ^b , 1 ^{bc} , 2.1 ^c)

Tab. 4: Comparisons of species similarity (Jaccard index) of ant assemblages of the timber tree *Tabebuia rosea*, planted in a pasture afforestation system in monocultures (MON) and three species mixtures (MIX), and in a silvopastoral system, where *T. rosea* was planted surrounded by five individuals of the companion tree species *Guazuma ulmifolia* (TGua), or *Gliricidia sepium* (TGli), or as solitary trees.

Branch samplings		Pasture afforestation		Silvopastoral		
		MON	MIX	TGua	TGli	TSol
Pasture afforestation	MON	–	0.294	0.333	0.350	0.250
	MIX	–	–	0.579	0.435	0.409
Silvopastoral	TGua	–	–	–	0.750	0.731
	TGli	–	–	–	–	0.636
	TSol	–	–	–	–	–
Baits						
Pasture afforestation	MON	–	0.750	0.625	0.643	0.667
	MIX	–	–	0.438	0.538	0.700
Silvopastoral	TGua	–	–	–	0.563	0.571
	TGli	–	–	–	–	0.583
	TSol	–	–	–	–	–

Tabebuia rosea was dissimilar among planting schemes (Tab. 4). Regarding the branch sample data, comparisons of the Jaccard similarity values of the ant assemblages on *T. rosea* in the different planting schemes indicated highest similarities among the planting schemes of the silvopastoral system, specifically among TGua and TGli trees (Tab. 4). The lowest similarities were observed among monocultures (pasture afforestation system) and all other planting schemes (Tab. 4). Considering the ant assemblages recorded at baits, we observed the highest similarity among ant assemblages of *T. rosea* individuals growing in monocultures and mixtures within the pasture afforestation system (Tab. 4). Comparisons of similarity between individual trees among planting schemes revealed signifi-

cant differences of the ant assemblages recorded by branch sampling in the silvopastoral system ($H = 15.3$, $P < 0.001$). Ant assemblages of *T. rosea* were significantly less similar within TSol trees than within TGua ($P = 0.004$) or TGli trees ($P < 0.001$). The similarity of the ant assemblages on *T. rosea* trees did not differ significantly between TGua and TGli trees ($P = 0.551$). All further comparisons of species similarity between individual trees among planting schemes were not significant (all $P > 0.05$).

Nest density of *Ectatomma ruidum* and *Camponotus lindigi*: In the pasture afforestation system we recorded a median nest density of *E. ruidum* of 0.88 nests / m² (one nest per observation circle) in monocultures and 1.77 nests / m² in mixtures (Fig. 4). Median nest density of *C. lin-*

digi was 0 nests / m² in both planting schemes (Fig. 4). Nest densities of *E. ruidum* ($U = 1655.5$, $P = 0.437$) and *C. lindigi* ($U = 1680$, $P = 0.285$) did not differ among mixed tree stands and monocultures but were significantly and negatively related to one another ($\chi^2_1 = 9.62$, $P = 0.002$).

In the silvopastoral system, median nest density of *Ectatomma ruidum* was 0.88 nests / m² at TGua trees and 0 nests / m² at TGli trees, TSol trees, and within the open pasture (Fig. 4). Median nest density of *Camponotus lindigi* was 0 nests / m² in all planting schemes (Fig. 4). We never recorded more than one nest of *C. lindigi* per observation circle, resulting in a maximum recorded nest density of 0.88 nests / m². Nest densities of *E. ruidum* ($H = 2.23$, $P = 0.328$) and *C. lindigi* ($H = 1.83$, $P = 0.401$) did not differ among planting schemes. Nest density of *E. ruidum* was low around sticks set up in the pasture (Fig. 4) but not significantly lower than the nest density recorded around *T. rosea* trees (all $P > 0.05$). Nest density of *C. lindigi* was significantly lower in the pasture than around TSol trees ($U = 329.0$, $P = 0.026$) and TGli trees ($U = 310.0$, $P = 0.021$). Nest densities of *E. ruidum* and *C. lindigi* were not related to each other in the silvopastoral system ($\chi^2_1 = 0.05$, $P = 0.819$).

Discussion

In this study we assessed the diversity of ant assemblages associated with the native timber tree *Tabebuia rosea* established on degraded tropical pasture, three to five years after tree planting. We found moderately diverse ant assemblages that are dominated by ground-nesting species, and that ant diversity can be affected by planting schemes and may be positively related to tree stand diversity.

Effects of tree stand diversity on ant diversity: In the pasture afforestation system, *Tabebuia rosea* individuals growing in mixtures supported a higher ant species richness, a higher ICE (estimated species richness), and a higher Simpson index than *T. rosea* individuals growing in monocultures, as we found in branch samples and at baits. This result is new for tropical timber tree plantations and it parallels findings from tropical coffee and cocoa agroforestry systems, where ant diversity was found to be positively related to the diversity of shade trees and habitat (PERFECTO & al. 1997, ARMBRECHT & PERFECTO 2003, BISSELEUA & al. 2009). Furthermore, our results demonstrate that although tree species identity is certainly a relevant factor for arthropod diversity (VEHVILAINEN & al. 2008, PLATH & al. 2012a), tree stand diversity can also contribute to increased ant diversity. Ant assemblage composition in our study was similar at baits across monocultures and mixtures, suggesting that competitive ant species might have been attracted into the plots of both planting schemes. However, assemblage composition showed low similarity in branch samples between monocultures and mixtures, demonstrating effects of habitat complexity on these assemblages. The enemy hypothesis states that increased habitat complexity leads to greater abundances and diversity of natural enemies, due to a greater diversity of prey and microhabitats and the presence of alternative feeding sources, such as nectar or pollen (ROOT 1973, BARBOSA & al. 2009). Therefore the observed higher ant diversity in species mixtures might be related to the more heterogeneous environment leading to a greater variety and amount of resources for ants (ARMBRECHT & al. 2004), or

to more favorable microclimatic conditions or ground cover (ACHURY & al. 2012). Overall, planting timber trees in species mixtures can facilitate higher productivity through nitrogen fixation and complementary resource use (FORRESTER & al. 2006, KELTY 2006, DAUDIN & SIERRA 2008, POTVIN & GOTELLI 2008). Therefore positive effects of mixtures on biodiversity might go hand in hand with economic benefits.

Effects of companion trees on ant diversity: In the silvopastoral system, *Tabebuia rosea* individuals surrounded by companion trees supported higher species richness than solitary *T. rosea* trees, as we recorded at baits on the tree trunks. Furthermore, ICE of *T. rosea* trees surrounded by *Gliricidia sepium* was higher than ICE of solitary *T. rosea* trees. Similar as in the pasture afforestation system, this higher ant diversity in the more diversified system, here in the presence of companion trees, might be due to a reduction of interspecific competition associated with the greater habitat heterogeneity, allowing more species to co-exist (SPERBER & al. 2004, DELABIE & al. 2007). Furthermore, companion trees affect the microclimate of the central timber tree by altering light and drought conditions through shading (GUTBRODT & al. 2011, RIEDEL & al. 2013b), possibly resulting in reduced thermal stress for ants (BESTELMEYER 2000, MCGLYNN & al. 2010, WIESCHER & al. 2012). Remarkably, both native companion tree species generated these assumedly favorable environmental effects irrespective of their species identity. Ant species richness was higher with than without their presence, and ant assemblage composition as recorded by branch samplings was most similar among *T. rosea* individuals associated with the two companion tree species. These findings underline the expectation that such beneficial effects of companion trees might be little affected by species identity, and encourage testing of further candidate companion tree species. In addition to diversity-enhancing effects, companion trees may support timber tree growth and provide additional goods, such as shade for cattle and fodder in the dry season (GAREN & al. 2011, PLATH & al. 2011a, RIEDEL & al. 2013b). Furthermore, association of timber trees with companion trees in living fences can protect the timber trees from livestock trampling in pastures (LOVE & al. 2009). Therefore, similar to the pasture afforestation system, the commercial benefit of companion trees goes along with the support of biodiversity.

Ant diversity in tropical native timber tree plantations on former pasture: Overall, we recorded 22 ant species in the pasture afforestation system and 28 ant species in the silvopastoral system using different sampling methods. The ant assemblage in the tree crowns and at baits on the tree trunk of *Tabebuia rosea* was dominated by *Ectatomma ruidum* and *Camponotus lindigi*. Additionally, the tropical fire ant *Solenopsis geminata* occurred sporadically but in high individual numbers at baits, predominantly in the silvopastoral system. *Solenopsis geminata* is a pugnacious ground nesting ant native and common in Central and South America, which often dominates natural as well as agricultural ecosystems, especially where land use intensification has created open areas with high solar insolation (RISCH & CARROLL 1982, NESTEL & DICKSCHEN 1990, WETTERER 2011). *Ectatomma ruidum* is also a common ground-nesting generalist that inhabits a variety of habitats, including open pastures (WEBER 1946, ZELIKOVA

& BREED 2008). Little specific information exists on the biology of *C. lindigi*. However, the subdominant *C. atriceps* (SMITH, 1858) was studied in Costa Rica by LONGINO (2013), who observed that it is abundant in secondary growth and areas of high insolation, nesting in twigs on trees or on the ground. This dominance of ground-nesting and generalist species, which are capable to tolerate habitat disturbance, probably reflects the preceding land use of the study site that has been used intensively as cattle pasture for 50 years before the native tree plantation was established (POTVIN & al. 2004). In tropical agro-ecosystems the degree of habitat disturbance and isolation seems to be crucial in determining the structure of prevailing ant communities as ant diversity has been found to decrease with land use intensity and distance to natural structures (TEODORO & al. 2011, ACHURY & al. 2012). Whereas tropical agroforests like shade cocoa plantations can harbor a diverse ant fauna similar to native habitats (DELABIE & al. 2007, PHILPOTT & al. 2008), the ant fauna of tropical pastures has a comparatively low diversity that might be similar to that of urban areas (DELABIE & al. 2007, OTTONETTI & al. 2010, ACHURY & al. 2012). Despite of the dominance of disturbance-related species, we also recorded forest species including *Pseudomyrmex gracilis* (FABRICIUS, 1804) (WARD 1993) and *P. oculatus* (SMITH, 1855) (WARD 1989) as well as the keystone species *Eciton burchellii*, which is associated with more than 300 species of arthropods and birds (MEISEL 2006, RETTENMEYER & al. 2011). Thus, beyond improving habitat quality for ground nesting species, the plantations provide a habitat for tree-dependent species, which may be of interest when considering the conservation value of tree re-establishment on former pasture.

Comparing the two planting systems, notable differences became apparent. In agreement with the findings of BOS & al. (2007), we recorded higher ant species diversity in the open silvopastoral system compared to the densely reforested pasture afforestation system, caused by a higher number of non-forest ant species in the open area, including *Wasmannia auropunctata* (see ACHURY & al. 2012) and *Dolichoderus bispinosus* (see MACKAY 1993). This result supports the finding that open land use types like pastures contain arthropod communities that are distinct from shaded systems like forests and agroforests (TEODORO & al. 2011, SCHMIDT & al. 2013). For *Ectatomma ruidum*, we found a higher nest density in the pasture afforestation system than in the silvopastoral system, contrasting a report that recorded higher nest density in treeless pastures than in tree containing pastures (SANTAMARIA & al. 2009). However, in line with our results, MCGLYNN & al. (2010) characterized *E. ruidum* as a "thermophile in the shade" with a clear preference for shaded nesting sites in behavioral experiments. The conclusions of these authors are further corroborated by our finding that in the silvopastoral system *E. ruidum* nests were concentrated around *Tabebuia rosea* trees associated with the large *Guzuma ulmifolia* companion trees (RIEDEL & al. 2013b). Furthermore, the overall high nest density of *E. ruidum* demonstrates the ability of this species to saturate its environment, which is of advantage in biological control (LEVINGS & FRANKS 1982, BREED & al. 1990). *Ectatomma ruidum* was among the dominant ant species in studies that detected ant-mediated plant protection (BENTLEY 1976,

DE LA FUENTE & MARQUIS 1999). Yet, we found only a weak negative relation of *E. ruidum* presence and leaf damage of *T. rosea* in a previous study at the site (RIEDEL & al. 2013a). In the pasture afforestation system, the presence of *E. ruidum* nests was negatively related to the presence of *C. lindigi* nests, constituting a mosaic like structure, a situation observed frequently in tree plantations that are characterized by a comparably simple canopy structure (MAJER & al. 1994, RIBEIRO & al. 2013).

Temporal changes in ant abundance and diversity with progressing season and tree age: Our finding of strong seasonal variation in ant abundance and diversity emphasizes that it might be advisable to record ant diversity repeatedly and over a longer time period to sample the ant community as completely as possible (HERBERS 2011). Ant diversity did not decrease over time, indicating that habitat complexity was sufficient to allow the prolonged coexistence of several species within the plantation (CERDÁ & al. 2013). Over time, as trees grow and provide further nesting sites like cavities or epiphytes, ant species diversity might further increase (BLÜTHGEN & al. 2000). However, colonization by further species depends on the presence of relict species in the vicinity that are able to migrate into the plantation. Therefore afforestation should consider habitat connectivity with links from remnant forest trees or forest fragments (MAJER & DELABIE 1999, BOS & al. 2007).

Conclusions

Native tree plantations on tropical pastures can sustain moderately diverse ant assemblages, dominated by ground nesting, disturbance tolerant species, while also providing habitat to forest species. In high density afforestation systems, tree species mixtures may support a greater ant diversity through increased habitat heterogeneity. Similarly, in silvopastoral systems, the association of timber trees with multipurpose companion trees holds potential to increase ant diversity. Since tree species mixtures and companion tree planting can also provide economic benefits to small-scale farmers, applying such planting systems is promising to reconcile the needs of landowners with the conservation of biodiversity.

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References

ACHURY, R., ULLOA, P.C. de & ARCILA, A. 2012: Effects of the heterogeneity of the landscape and the abundance of *Wasmannia auropunctata* on ground ant assemblages in a Co-

- lombian tropical dry forest. – *Psyche: A Journal of Entomology* 2012: 960475.
- ANDERSEN, A.N. & MAJER, J.D. 2004: Ants show the way Down Under: invertebrates as bioindicators in land management. – *Frontiers in Ecology and the Environment* 2: 291-298.
- ARMBRECHT, I. & PERFECTO, I. 2003: Litter-twig dwelling ant species richness and predation potential within a forest fragment and neighboring coffee plantations of contrasting habitat quality in Mexico. – *Agriculture Ecosystems & Environment* 97: 107-115.
- ARMBRECHT, I., PERFECTO, I. & VANDERMEER, J. 2004: Enigmatic biodiversity correlations: ant diversity responds to diverse resources. – *Science* 304: 284-286.
- BARBOSA, P., HINES, J., KAPLAN, I., MARTINSON, H., SZCZEPANIEC, A. & SZENDREI, Z. 2009: Associational resistance and associational susceptibility: having right or wrong neighbors. – *Annual Review of Ecology Evolution and Systematics* 40: 1-20.
- BENTLEY, B.L. 1976: Plants bearing extrafloral nectaries and associated ant community: interhabitat differences in reduction of herbivore damage. – *Ecology* 57: 815-820.
- BESTELMEYER, B.T. 2000: The trade-off between thermal tolerance and behavioural dominance in a subtropical South American ant community. – *Journal of Animal Ecology* 69: 998-1009.
- BISSELEUA, D.H.B., MISSOUP, A.D. & VIDAL, S. 2009: Biodiversity conservation, ecosystem functioning, and economic incentives under cocoa agroforestry intensification. – *Conservation Biology* 23: 1176-1184.
- BLÜTHGEN, N., MEZGER, D. & LINSINMAIR, K.E. 2006: Ant-hemipteran trophobioses in a Bornean rainforest – diversity, specificity and monopolisation. – *Insectes Sociaux* 53: 194-203.
- BLÜTHGEN, N., VERHAAGH, M., GOITIA, W. & BLÜTHGEN, N. 2000: Ant nests in tank bromeliads – an example of non-specific interaction. – *Insectes Sociaux* 47: 313-316.
- BOLTON, B. 1994: Identification guide to the ant genera of the world. – Harvard University Press, Cambridge, MA, 222 pp.
- BOS, M.M., STEFFAN-DEWENTER, I. & TSCHARNTKE, T. 2007: The contribution of cacao agroforests to the conservation of lower canopy ant and beetle diversity in Indonesia. – *Biodiversity and Conservation* 16: 2429-2444.
- BREED, M.D., ABEL, P., BLEUZE, T.J. & DENTON, S.E. 1990: Thievery, home ranges, and nestmate recognition in *Ectatomma ruidum*. – *Oecologia* 84: 117-121.
- BROCKERHOFF, E.G., JACTEL, H., PARROTTA, J.A., QUINE, C.P. & SAYER, J. 2008: Plantation forests and biodiversity: oxymoron or opportunity? – *Biodiversity and Conservation* 17: 925-951.
- CAJAS-GIRON, Y.S. & SINCLAIR, F.L. 2001: Characterization of multistrata silvopastoral systems on seasonally dry pastures in the Caribbean Region of Colombia. – *Agroforestry Systems* 53: 215-225.
- CERDÁ, X., ARNAN, X. & RETANA, J. 2013: Is competition a significant hallmark of ant (Hymenoptera: Formicidae) ecology? – *Myrmecological News* 18: 131-147.
- CHAO, A., HWANG, W.H., CHEN, Y.C. & KUO, C.Y. 2000: Estimating the number of shared species in two communities. – *Statistica Sinica* 10: 227-246.
- COLWELL, R.K. 2013: EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. – <<http://purl.oclc.org/estimates>>, retrieved on 27 May 2013.
- CRIST, T.O. 2009: Biodiversity, species interactions, and functional roles of ants (Hymenoptera: Formicidae) in fragmented landscapes: a review. – *Myrmecological News* 12: 3-13.
- DAGANG, A.B.K. & NAIR, P.K.R. 2003: Silvopastoral research and adoption in Central America: recent findings and recommendations for future directions. – *Agroforestry Systems* 59: 149-155.
- DAUDIN, D. & SIERRA, J. 2008: Spatial and temporal variation of below-ground N transfer from a leguminous tree to an associated grass in an agroforestry system. – *Agriculture Ecosystems & Environment* 126: 275-280.
- DE LA FUENTE, M.A.S. & MARQUIS, R.J. 1999: The role of ant-tended extrafloral nectaries in the protection and benefit of a neotropical rainforest tree. – *Oecologia* 118: 192-202.
- DELABIE, J.H.C., JAHYNY, B., DO NASCIMENTO, I.C., MARIANO, C.S.F., LACAU, S., CAMPIOLO, S., PHILPOTT, S.M. & LEPONCE, M. 2007: Contribution of cocoa plantations to the conservation of native ants (Insecta: Hymenoptera: Formicidae) with a special emphasis on the Atlantic Forest fauna of southern Bahia, Brazil. – *Biodiversity and Conservation* 16: 2359-2384.
- DELAGRANGE, S., POTVIN, C., MESSIER, C. & COLL, L. 2008: Linking multiple-level tree traits with biomass accumulation in native tree species used for reforestation in Panama. – *Trees-Structure and Function* 22: 337-349.
- DIAZ-CASTELAZO, C., RICO-GRAY, V., ORTEGA, F. & ANGELES, G. 2005: Morphological and secretory characterization of extrafloral nectaries in plants of coastal Veracruz, Mexico. – *Annals of Botany* 96: 1175-1189.
- DORROUGH, J., MCINTYRE, S., BROWN, G., STOL, J., BARRETT, G. & BROWN, A. 2012: Differential responses of plants, reptiles and birds to grazing management, fertilizer and tree clearing. – *Austral Ecology* 37: 569-582.
- ELLISON, A.M. 2012: Out of Oz: opportunities and challenges for using ants (Hymenoptera: Formicidae) as biological indicators in north-temperate cold biomes. – *Myrmecological News* 17: 105-119.
- ERSKINE, P.D., LAMB, D. & BRISTOW, M. 2006: Tree species diversity and ecosystem function: can tropical multi-species plantations generate greater productivity? – *Forest Ecology and Management* 233: 205-210.
- FAO 2009: The state of food and agriculture, livestock in the balance. – FAO, Rome, 166 pp.
- FERNÁNDEZ, F. 2003: Introducción a las hormigas de la región Neotropical. – Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, 424 pp.
- FLOREN, A., BIUN, A. & LINSINMAIR, K.E. 2002: Arboreal ants as key predators in tropical lowland rainforest trees. – *Oecologia* 131: 137-144.
- FOLGARAIT, P.J., MARQUIS, R.J., INGVARSSON, P., BRAKER, H.E. & ARGUEDAS, M. 1995: Patterns of attack by insect herbivores and a fungus on saplings in a tropical tree plantation. – *Environmental Entomology* 24: 1487-1494.
- FORRESTER, D.I., BAUHUS, H. & COWIE, A.L. 2005: On the success and failure of mixed-species tree plantations: lessons learned from a model system of *Eucalyptus globulus* and *Acacia mearnsii*. – *Forest Ecology and Management* 209: 147-155.
- FORRESTER, D.I., BAUHUS, J., COWIE, A.L. & VANCLAY, J.K. 2006: Mixed-species plantations of *Eucalyptus* with nitrogen-fixing trees: a review. – *Forest Ecology and Management* 233: 211-230.
- GAREN, E.J., SALTONSTALL, K., ASHTON, M.S., SLUSSER, J.L., MATHIAS, S. & HALL, J.S. 2011: The tree planting and protecting culture of cattle ranchers and small-scale agriculturalists in rural Panama: opportunities for reforestation and land restoration. – *Forest Ecology and Management* 261: 1684-1695.
- GARRITY, D.P. 2004: Agroforestry and the achievement of the millennium development goals. – *Agroforestry Systems* 61: 5-17.
- GENTRY, A.H. 1970: A revision of *Tabebuia rosea* (Bignoniaceae) in Central America. – *Brittonia* 22: 246-264.

- GENTRY, A.H. 1973: Flora of Panama. Part 9. Family 172. Bignonaceae. – *Annals of the Missouri Botanical Garden* 60: 781-977.
- GORDON, C.E., MCGILL, B., IBARRA-NUNEZ, G., GREENBERG, R. & PERFECTO, I. 2009: Simplification of a coffee foliage-dwelling beetle community under low-shade management. – *Basic and Applied Ecology* 10: 246-254.
- GOTELLI, N.J., ELLISON, A.M., DUNN, R.R. & SANDERS, N.J. 2011: Counting ants (Hymenoptera: Formicidae): biodiversity sampling and statistical analysis for myrmecologists. – *Myrmecological News* 15: 13-19.
- GRAHAM, P.H. & VANCE, C.P. 2003: Legumes: importance and constraints to greater use. – *Plant Physiology* 131: 872-877.
- GRAU, H.R. & AIDE, M. 2008: Globalization and land-use transitions in Latin America. – *Ecology and Society* 13: 16.
- GUTBRODT, B., MODY, K. & DORN, S. 2011: Drought changes plant chemistry and causes contrasting responses in lepidopteran herbivores. – *Oikos* 120: 1732-1740.
- HALL, J.M., VAN HOLT, T., DANIELS, A.E., BALTHAZAR, V. & LAMBIN, E.F. 2012: Trade-offs between tree cover, carbon storage and floristic biodiversity in reforesting landscapes. – *Landscape Ecology* 27: 1135-1147.
- HALL, J.S., ASHTON, M.S., GAREN, E.J. & JOSE, S. 2011a: The ecology and ecosystem services of native trees: implications for reforestation and land restoration in Mesoamerica. – *Forest Ecology and Management* 261: 1553-1557.
- HALL, J.S., LOVE, B.E., GAREN, E.J., SLUSSER, J.L., SALTONSTALL, K., MATHIAS, S., VAN BREUGEL, M., IBARRA, D., BORK, E.W., SPANER, D., WISHNIE, M.H. & ASHTON, M.S. 2011b: Tree plantations on farms: evaluating growth and potential for success. – *Forest Ecology and Management* 261: 1675-1683.
- HARTLEY, M.J. 2002: Rationale and methods for conserving biodiversity in plantation forests. – *Forest Ecology and Management* 155: 81-95.
- HARVEY, C.A., MEDINA, A., MERLO SANCHEZ, D., VILCHEZ, S., HERNANDEZ, B., SAENZ, J.C., MAES, J.M., CASANOVES, F. & SINCLAIR, F.L. 2006: Patterns of animal diversity in different forms of tree cover in agricultural landscapes. – *Ecological Applications* 16: 1986-1999.
- HERBERS, J.M. 2011: Nineteen years of field data on ant communities (Hymenoptera: Formicidae): What can we learn? – *Myrmecological News* 15: 43-52.
- HOFFMANN, B.D. 2010: Using ants for rangeland monitoring: global patterns in the responses of ant communities to grazing. – *Ecological Indicators* 10: 105-111.
- HÖLDOBLER, B. & WILSON, E.O. 1990: *The ants*. – Belknap Press of Harvard University Press, Cambridge, MA, 732 pp.
- JACTEL, H., BROCKERHOFF, E. & DUELLI, P. 2005: A test of the biodiversity-stability theory: meta-analysis of tree species diversity effects on insect pest infestations, and re-examination of responsible factors. – *Forest Diversity and Function: Temperate and Boreal Systems* 176: 235-262.
- KELTY, M.J. 2006: The role of species mixtures in plantation forestry. – *Forest Ecology and Management* 233: 195-204.
- KOPONEN, S. 2004: Arthropods from high oak branches – comparison of two trap types, with a special reference to spiders. – *Latvijas Entomologs* 41: 71-75.
- LAMB, D., ERSKINE, P.D. & PARROTTA, J.A. 2005: Restoration of degraded tropical forest landscapes. – *Science* 310: 1628-1632.
- LETOURNEAU, D.K., ARMBRECHT, I., SALGUERO RIVERA, B., MONTROYA LERMA, J., JIMENEZ CARMONA, E., CONSTANZA DAZA, M., ESCOBAR, S., GALINDO, V., GUTIERREZ, C., DUQUE LOPEZ, S., LOPEZ MEJIA, J., ACOSTA RANGEL, A.M., HERRERA RANGEL, J., RIVERA, L., ARTURO SAAVEDRA, C., MARINA TORRES, A. & REYES TRUJILLO, A. 2011: Does plant diversity benefit agroecosystems? A synthetic review. – *Ecological Applications* 21: 9-21.
- LEVINGS, S.C. & FRANKS, N.R. 1982: Patterns of nest dispersion in a tropical ground ant community. – *Ecology* 63: 338-344.
- LONGINO, J. 2013: *Camponotus atriceps* in Costa Rica. – <http://www.antweb.org/description.do?name=atriceps&genus=Camponotus&project=louisianaants>, retrieved on 5 June 2013.
- LOVE, B.E., BORK, E.W. & SPANER, D. 2009: Tree seedling establishment in living fences: a low-cost agroforestry management practice for the tropics. – *Agroforestry Systems* 77: 1-8.
- LUDWIG, J.A. & REYNOLDS, J.F. 1988: *Statistical ecology, a primer on methods and computing*. – John Wiley & Sons, NY, 337 pp.
- MACKAY, W.P. 1993: A review of the New World ants of the genus *Dolichoderus* (Hymenoptera: Formicidae). – *Sociobiology* 22: 1-143.
- MAGURRAN, A.E. 2004: *Measuring biological diversity*. – Blackwell Science, Oxford, UK, 256 pp.
- MAJER, J.D. & DELABIE, J.H.C. 1999: Impact of tree isolation on arboreal and ground ant communities in cleared pasture in the Atlantic rain forest region of Bahia, Brazil. – *Insectes Sociaux* 46: 281-290.
- MAJER, J.D., DELABIE, J.H.C. & SMITH, M.R.B. 1994: Arboreal ant community patterns in Brazilian cocoa farms. – *Biotropica* 26: 73-83.
- MCGLYNN, T.P., DUNN, T., WAYMAN, E. & ROMERO, A. 2010: A thermophile in the shade: light-directed nest relocation in the Costa Rican ant *Ectatomma ruidum*. – *Journal of Tropical Ecology* 26: 559-562.
- MEISEL, J.E. 2006: Thermal ecology of the neotropical army ant *Eciton burchellii*. – *Ecological Applications* 16: 913-922.
- MODY, K. & LINSENMAYER, K.E. 2004: Plant-attracted ants affect arthropod community structure but not necessarily herbivory. – *Ecological Entomology* 29: 217-225.
- MURGUEITIO, E., CALLE, Z., URIBE, F., CALLE, A. & SOLORIO, B. 2011: Native trees and shrubs for the productive rehabilitation of tropical cattle ranching lands. – *Forest Ecology and Management* 261: 1654-1663.
- NESTEL, D. & DICKSCHEN, F. 1990: The foraging kinetics of ground ant communities in different Mexican coffee agroecosystems. – *Oecologia* 84: 58-63.
- OTTONETTI, L., TUCCI, L., FRIZZI, F., CHELAZZI, G. & SANTINI, G. 2010: Changes in ground-foraging ant assemblages along a disturbance gradient in a tropical agricultural landscape. – *Ethology Ecology & Evolution* 22: 73-86.
- PERFECTO, I., VANDERMEER, J., HANSON, P. & CARTIN, V. 1997: Arthropod biodiversity loss and the transformation of a tropical agro-ecosystem. – *Biodiversity and Conservation* 6: 935-945.
- PHILPOTT, S.M. & ARMBRECHT, I. 2006: Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function. – *Ecological Entomology* 31: 369-377.
- PHILPOTT, S.M., PERFECTO, I. & VANDERMEER, J. 2008: Effects of predatory ants on lower trophic levels across a gradient of coffee management complexity. – *Journal of Animal Ecology* 77: 505-511.
- PINHEIRO, J.C. & BATES, D.M. 2000: *Mixed-effects models in S and S-PLUS*. – Springer, New York, 530 pp.
- PIOTTO, D., CRAVEN, D., MONTAGNINI, F. & ALICE, F. 2010: Silvicultural and economic aspects of pure and mixed native tree species plantations on degraded pasturelands in humid Costa Rica. – *New Forests* 39: 369-385.

- PLATH, M., DORN, S., BARRIOS, H. & MODY, K. 2012a: Diversity and composition of arboreal beetle assemblages in tropical pasture afforestations: effects of planting schemes and tree species identity. – *Biodiversity Conservation* 21: 3423-3444.
- PLATH, M., DORN, S., RIEDEL, J., BARRIOS, H. & MODY, K. 2012b: Associational resistance and associational susceptibility: specialist herbivores show contrasting responses to tree stand diversification. – *Oecologia* 169: 477-487.
- PLATH, M., MODY, K., POTVIN, C. & DORN, S. 2011a: Do multipurpose companion trees affect high value timber trees in a silvopastoral plantation system? – *Agroforestry Systems* 81: 79-92.
- PLATH, M., MODY, K., POTVIN, C. & DORN, S. 2011b: Establishment of native tropical timber trees in monoculture and mixed-species plantations: small-scale effects on tree performance and insect herbivory. – *Forest Ecology and Management* 261: 741-750.
- POTVIN, C. & GOTELLI, N.J. 2008: Biodiversity enhances individual performance but does not affect survivorship in tropical trees. – *Ecology Letters* 11: 217-223.
- POTVIN, C., WHIDDEN, E. & MOORE, T. 2004: A case study of carbon pools under three different land-uses in Panama. – *Climatic Change* 67: 291-307.
- RETTENMEYER, C.W., RETTENMEYER, M.E., JOSEPH, J. & BERGHOF, S.M. 2011: The largest animal association centered on one species: the army ant *Eciton burchellii* and its more than 300 associates. – *Insectes Sociaux* 58: 281-292.
- RIBEIRO, S.P., ESPÍRITO SANTO, N.B., DELABIE, J.H.C. & MAJER, J.D. 2013: Competition, resources and the ant (Hymenoptera: Formicidae) mosaic: a comparison of upper and lower canopy. – *Myrmecological News* 18: 113-120.
- RIEDEL, J., DORN, S., BRAND, G., BARRIOS, H. & MODY, K. 2013a: Effects of ants on arthropod assemblages of a native timber tree in a reforestation plantation. – *Journal of Applied Entomology* 137: 418-428.
- RIEDEL, J., DORN, S., PLATH, M. & MODY, K. 2013b: Growth, herbivore distribution, and herbivore damage of timber trees in a tropical silvopastoral reforestation system. – *Annals of Forest Science* 70: 75-86.
- RIEDEL, J., DORN, S., PLATH, M., POTVIN, C. & MODY, K. 2013c: Time matters: temporally changing effects of planting schemes and insecticide treatment on native timber tree performance on former pasture. – *Forest Ecology and Management* 297: 49-56.
- RISCH, S.J. & CARROLL, C.R. 1982: The ecological role of ants in two Mexican agroecosystems. – *Oecologia* 55: 114-119.
- ROOT, R.B. 1973: Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). – *Ecological Monographs* 43: 95-120.
- ROSUMEK, F.B., SILVEIRA, F.A.O., NEVES, F.D., BARBOSA, N.P.D., DINIZ, L., OKI, Y., PEZZINI, F., FERNANDES, G.W. & CORNELISSEN, T. 2009: Ants on plants: a meta-analysis of the role of ants as plant biotic defenses. – *Oecologia* 160: 537-549.
- SANTAMARIA, C., ARMBRECHT, I. & LACHAUD, J.P. 2009: Nest distribution and food preferences of *Ectatomma ruidum* (Hymenoptera: Formicidae) in shaded and open cattle pastures of Colombia. – *Sociobiology* 53: 517-541.
- SCHMIDT, F.A., CARLA R. RIBAS, C.R., SCHOEREDER, H.J. 2013: How predictable is the response of ant assemblages to natural forest recovery? Implications for their use as bioindicators. – *Ecological Indicators* 24: 158-166.
- SMITH, F.P., PROBER, S.M., HOUSE, A.P.N. & MCINTYRE, S. 2013: Maximizing retention of native biodiversity in Australian agricultural landscapes – the 10:20:40:30 guidelines. – *Agriculture Ecosystems & Environment* 166: 35-45.
- SORVARI, J. 2009: Foraging distances and potentiality in forest pest insect control: an example with two candidate ants (Hymenoptera: Formicidae). – *Myrmecological News* 12: 211-215.
- SOUZA, A.F., RAMOS, N.P., PIZO, M.A., HUEBEL, I. & CROSSETTI, L.O. 2013: Afforestation effects on vegetation structure and diversity of grasslands in southern Brazil: the first years. – *Journal for Nature Conservation* 21: 56-62.
- SPERBER, C.F., NAKAYAMA, K., VALVERDE, M.J. & NEVES, F.D. 2004: Tree species richness and density affect parasitoid diversity in cacao agroforestry. – *Basic and Applied Ecology* 5: 241-251.
- STEPHENS, S.S. & WAGNER, M.R. 2007: Forest plantations and biodiversity: a fresh perspective. – *Journal of Forestry* 105: 307-313.
- STUNTZ, S., SIMON, U. & ZOTZ, G. 1999: Assessing the potential influence of vascular epiphytes on arthropod diversity in tropical tree crowns: hypotheses, approaches, and preliminary data. – *Selbyana* 20: 276-283.
- TAHVANAINEN, J.O. & ROOT, R.B. 1972: The influence of vegetational diversity on the population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). – *Oecologia* 10: 321-346.
- TANAKA, H.O., YAMANE, S. & ITIOKA, T. 2010: Within-tree distribution of nest sites and foraging areas of ants on canopy trees in a tropical rainforest in Borneo. – *Population Ecology* 52: 147-157.
- TEODORO, A.V., MUNOZ, A., TSCHARNTKE, T., KLEIN, A.M. & TYLIANAKIS, J.M. 2011: Early succession arthropod community changes on experimental passion fruit plant patches along a land-use gradient in Ecuador. – *Agriculture Ecosystems and Environment* 140: 14-19.
- TRAGER, J.C. 1991: A revision of the fire ants, *Solenopsis geminata* group (Hymenoptera: Formicidae: Myrmicinae). – *Journal of the New York Entomological Society* 99: 141-198.
- VAN BREUGEL, M., HALL, J.S., CRAVEN, D.J., GREGOIRE, T.G., PARK, A., DENT, D.H., WISHNIE, M.H., MARISCAL, E., DEAGO, J., IBARRA, D., CEDENÑO, N. & ASHTON, M.S. 2011: Early growth and survival of 49 tropical tree species across sites differing in soil fertility and rainfall in Panama. – *Forest Ecology and Management* 261: 1580-1589.
- VANDERMEER, J. & PERFECTO, I. 2007: The agricultural matrix and a future paradigm for conservation. – *Conservation Biology* 21: 274-277.
- VEHVILAINEN, H., KORICHEVA, J. & RUOHOMAKI, K. 2007: Tree species diversity influences herbivore abundance and damage: meta-analysis of long-term forest experiments. – *Oecologia* 152: 287-298.
- VEHVILAINEN, H., KORICHEVA, J. & RUOHOMAKI, K. 2008: Effects of stand tree species composition and diversity on abundance of predatory arthropods. – *Oikos* 117: 935-943.
- VERHOEVEN, K.J.F., SIMONSEN, K.L. & MCINTYRE, L.M. 2005: Implementing false discovery rate control: increasing your power. – *Oikos* 108: 643-647.
- WARD, P.S. 1989: Systematic studies on pseudomyrmecine ants: revision of the *Pseudomyrmex oculatus* and *P. subtilissimus* species groups, with taxonomic comments on other species. – *Quaestiones Entomologicae* 25: 393-468.
- WARD, P.S. 1993: Systematic studies on *Pseudomyrmex* acacia-ants (Hymenoptera: Formicidae: Pseudomyrmecinae). – *Journal of Hymenoptera Research* 2: 117-168.
- WARDHAUGH, C.W., STORK, N.E. & EDWARDS, W. 2012: Feeding guild structure of beetles on Australian tropical rainforest trees reflects microhabitat resource availability. – *Journal of Animal Ecology* 81: 1086-1094.

- WASSENAAR, T., GERBER, P., VERBURG, P.H., ROSALES, M., IBRAHIM, M. & STEINFELD, H. 2007: Projecting land use changes in the Neotropics: the geography of pasture expansion into forest. – *Global Environmental Change-Human and Policy Dimensions* 17: 86-104.
- WEBER, N.A. 1946: Two common ponerine ants of possible economic significance, *Ectatomma tuberculatum* (OLIVIER) and *E. ruidum* ROGER. – *Proceedings of the Entomological Society of Washington* 48: 1-16.
- WETTERER, J.K. 2011: Worldwide spread of the tropical fire ant, *Solenopsis geminata* (Hymenoptera: Formicidae). – *Myrmecological News* 14: 21-35.
- WIESCHER, P.T., PEARCE-DUVET, J.M.C. & FEENER, D.H. 2012: Assembling an ant community: species functional traits reflect environmental filtering. – *Oecologia* 169: 1063-1074.
- WISHNIE, M.H., DENT, D.H., MARISCAL, E., DEAGO, J., CEDENO, N., IBARRA, D., CONDIT, R. & ASHTON, P.M.S. 2007: Initial performance and reforestation potential of 24 tropical tree species planted across a precipitation gradient in the Republic of Panama. – *Forest Ecology and Management* 243: 39-49.
- WOLF, S., EUGSTER, W., POTVIN, C. & BUCHMANN, N. 2011: Strong seasonal variations in net ecosystem CO₂ exchange of a tropical pasture and afforestation in Panama. – *Agricultural and Forest Meteorology* 151: 1139-1151.
- ZELIKOVA, T.J. & BREED, M.D. 2008: Effects of habitat disturbance on ant community composition and seed dispersal by ants in a tropical dry forest in Costa Rica. – *Journal of Tropical Ecology* 24: 309-316.