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Diversity and habitat use of understorey bats in forest and agroforestry systems at the margin of Lore Lindu National Park (Central Sulawesi, Indonesia)

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Verfasser: Stefan Graf

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Diversity and habitat use of understorey bats in forest and agroforestry systems at the margin of Lore Lindu National Park (Central Sulawesi, Indonesia)

Stefan Graf

Diploma Student at the Department of Animal Biodiversity, Faculty of Life Sciences,
University of Vienna, Rennweg 14, A-1030 Vienna, Austria

Abstract. Tropical landscapes are increasingly dominated by agriculture. However, still little is known about the contribution of land-use systems to preserving tropical biodiversity. Particularly, species that survive in forest remnants often interact closely with these agro-ecosystems. This study quantifies for the first time the importance of agroforestry systems in maintaining species diversity of forest understorey bats in Sulawesi, Indonesia. Therefore, we compared bat diversity of forest and cacao agroforestry systems and tested how changes in bat species assemblages are related to changes of structural habitat complexity. Bats were sampled by mist-netting in the understorey of natural forest, secondary forest and cacao agroforestry systems with a heterogeneous and a homogeneous shade tree layer (N = 4 replicate sites per habitat type) in Kulawi Valley at the western margin of Lore Lindu National Park. A total of 13 species were recorded during 8,592 net-meter-hours. The richness estimators Chao 2 and second-order Jackknife indicated a completeness of our species inventories of 62.2 and 79.8%, respectively. Abundances and species richness were greater in the understorey of agroforestry systems than in forests. Especially agroforestry systems with a diverse layer of shade trees (partly remaining from the formerly logged natural forest) and embedded in the forest margin appeared to harbor a high fraction of the local bat assemblage. Species composition did not differ between habitat types; rather bat assemblages appeared to be nested. However, results have to be interpreted cautiously due to the very small sample size achieved for our forest sites. Mean canopy closure and density of tall trees (dbh >50 cm) differed significantly between habitats. The abundance of two bat species (*Cynopterus brachyotis* and *Rousettus amplexicaudatus*) was negatively affected by increasing canopy closure; the abundance of one bat species (*Rousettus celebensis*) was negatively correlated with the number of tall trees. Other species showed at least a similar trend of decreasing abundances with increasing canopy closure and density of large trees. Our results suggest that cacao agroforestry systems have the potential to act as important feeding habitats for bats in the buffer zone of protected forest remnants in Indonesia.

Zusammenfassung Tropische Landschaften sind zunehmend durch landwirtschaftliche Flächen dominiert. Bis heute ist jedoch nur wenig bekannt, welchen Beitrag Landnutzungssystemen für den Erhalt tropischer Biodiversität leisten. Vor allem Arten in Waldfragmenten nutzen oftmals angrenzende Agroforstsysteme. In dieser Studie wird zum ersten Mal die Bedeutung dieser Landnutzungsform für Unterwuchs-Fledermausarten auf Sulawesi (Indonesien) quantifiziert. Dazu vergleichen wir die Fledermausvielfalt von Wäldern und Agroforstsystemen und testen welche Zusammenhänge zwischen Veränderungen der Fledermauszönosen und der strukturellen Habitatkomplexität bestehen. Die Freilandarbeiten wurden im Kulawi-Tal an der westlichen Grenze des Lore Lindu Nationalparks durchgeführt. Dort wurden mit Japannetzen insgesamt 13 Arten während 8.592 Netz-Meter-Stunden im Unterwuchs von Naturwäldern, Sekundärwäldern und Kakao-Agroforstsystemen mit einer von Schattenbäumen gebildeten, heterogenen bzw. sehr einförmigen Kronenschicht (N = 4 Repliken pro Habitattyp) gefangen. Das entspricht 62.2 bzw. 79.8% der geschätzten Artenvielfalt (Chao 2 bzw. second-order Jackknife). Sowohl Individuen- als auch Artenzahlen waren in den Agroforstsystemen höher als in den Wäldern. Vor allem nahe am Waldrand liegende Agroforstsysteme mit verschiedenen Schattenbäumen (Reste ehemaliger Naturwaldbäume) schienen von einem großen Anteil der vorhandenen Fledermausarten genutzt zu werden. Es konnten keine Unterschiede in der Artenzusammensetzung der einzelnen Habitattypen gefunden werden. Aufgrund der geringen Fangzahlen an den Waldstandorten sind diese Ergebnisse jedoch mit Vorsicht zu interpretieren. Die einzelnen Habitattypen unterschieden sich signifikant hinsichtlich Kronenschluss und der Anzahl großer Bäume (dbh >50 cm). Die Häufigkeit von zwei Fledermausarten (*Cynopterus brachyotis* und *Rousettus amplexicaudatus*) nahm mit zunehmendem Kronenschluss ab, die Fangrate einer weiteren Art (*Rousettus celebensis*) war negativ mit der Anzahl großer Bäume korreliert. Auch bei anderen Arten waren derartige Tendenzen erkennbar. Unsere Ergebnisse lassen die Vermutung zu, dass in Indonesien Kakao-Agroforstsysteme wichtige Nahrungshabitate für Fledermäuse in der Pufferzone um verbleibende Waldresten darstellen können.

Introduction

The ongoing deforestation is the main reason for the dramatic loss of tropical forests (Geist and Lambin 2002). Meanwhile landscapes throughout the tropics are dominated by agriculture, especially in Southeast Asia (Achard *et al.* 2002), a major biodiversity hotspot (Myers *et al.* 2000). A real cacao boom during the last two decades has intensified this process in Indonesia, particularly on the island of Sulawesi (Rice and Greenberg 2000, Potter 2001, Sunderlin *et al.* 2001, Clough *et al.* 2009). Many studies already focused on the impact of forest conversion to cacao agroforests on the diversity of various animal groups, including ants (Perfecto *et al.* 2003, Armbrecht *et al.* 2004), bees and wasps (Klein *et al.* 2002, Tylianakis *et al.* 2006), butterflies (Perfecto *et al.* 2003, Schulze *et al.* 2004a), beetles (Perfecto *et al.* 1997, Schulze *et al.* 2004b), frogs and lizards (Faria *et al.* 2007), birds (Perfecto *et al.* 2003, Waltert *et al.* 2004, Abrahamczyk *et al.* 2008) and bats (Faria *et al.* 2006, Faria and Baumgarten 2007). However, the relevance of agroforestry systems for biodiversity conservation is still controversial. While tropical agroforestry systems may represent the only human-dominated habitat with a considerable tree cover (Schroth *et al.* 2004), they are increasingly subject to shade tree management, including reduction in shade tree diversity or even the complete removal of shade canopies to increase yields of the main crops (Belsky and Siebert 2003, Zuidema *et al.* 2005, Steffan-Dewenter *et al.* 2007, Clough *et al.* 2009).

In general, disturbance and conversion of rainforests have a negative impact on tropical biodiversity, but the response to forest modification and land-use can differ between taxonomic groups (Lawton *et al.* 1998, Schulze *et al.* 2004b, Pineda *et al.* 2005, Faria *et al.* 2007, Cassano *et al.* 2009). Certain agroforestry systems are able to maintain a high proportion of forest species (Rice and Greenberg 2000, Hughes *et al.* 2002, Donald 2004, Faria *et al.* 2006) including bats (Faria and Baumgarten 2007, Harvey and González Villalobos 2007). Studies from the Neotropics showed that cacao plantations with shade trees can be characterized by a bat abundance and richness similar to forest sites (Pineda *et al.* 2005, Faria and Baumgarten 2007, Cassano *et al.* 2009). However, although characterized by a high diversity, species composition of bat assemblages between agroforestry systems and forest can differ (Harvey and González Villalobos 2007), indicating that agroforestry

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systems are not forest surrogates for bats. Furthermore, the pure occurrence of individual species in human-modified habitats does not necessarily prove that they are of similar importance than forest habitats, as indicated by significant changes of relative abundances in Malaysian understorey fruit bats from forest towards land-use systems (Campbell *et al.* 2007). The potential of agroforestry systems to harbour forest-dwelling bat species is closely linked to the existence of nearby forest tracts that may act as a source for species populations (Faria and Baumgarten 2007, Cassano *et al.* 2009). Due to the ability of bats to fly several kilometers during a single night (Pineda *et al.* 2005), certain land-use systems may only be used temporarily during foraging. Tropical bats provide important ecological services such as seed dispersal and pollination (Corlett and Hau 2000, Ingle 2003, Muscarella and Fleming 2007, Fleming and Muchhala 2008) and different feeding guilds (insectivores, frugivores and nectarivores) may respond differently to forest conversion and varying intensity of agroforest management.

In this study understorey bat assemblages of natural forest, selectively logged forest and cacao dominated agroforestry systems at the margin of Lore Lindu National Park in Central Sulawesi (Indonesia) were examined in order to determine effects of forest conversion and agroforest management intensity on taxonomic composition and diversity. Due to the ability of forests to act as a source area, we assumed that bat assemblages in agroforestry systems at the forest margin do not represent independent assemblages, but subsets of assemblages found in adjacent forest. Additionally, we predicted that vegetation density is particularly likely to be a key factor shaping bat species richness, because a certain fraction of bats may not be capable to penetrate dense understorey. Therefore we investigated the effects of forest understorey density on the occurrence of individual species. We furthermore expected that forest-dwelling species will respond especially sensitively to habitat degradation and will be suitable as indicators for forest disturbance. This study will provide data essential for evaluating the conservation relevance of agroforestry systems as buffer zone habitats at the margin of forest reserves.

Methods

Study area

The study was conducted around the village of Toro in the Kulawi Valley, Central Sulawesi, Indonesia (1°30'24" S, 120°2'11" E, 800-900 m asl). Toro is located at the western boundary of Lore Lindu National Park, about 100 kilometers south of Palu, the capital city of Central Sulawesi. The region has an annual average (± SE) temperature of 24.0 (± 0.16) °C and a mean monthly rainfall of 143.7 (± 22.74) mm (Bos *et al.* 2007). The area of the national park covers 231,000 ha of tropical lowland and montane rainforests and represents a regional biodiversity hotspot with a high rate of bat endemism (Whitten *et al.* 2002), possibly including still unknown species (Bates *et al.* 2007). The edge of Lore Lindu National Park is characterized by a mosaic of secondary forests, young fallows and land-use systems with cacao, coffee, maize and rice as dominating crops. A more detailed description of the study area is provided by Harteveld *et al.* (2007)

Site selection and measurement of habitat variables

All bat surveys took place on research plots established by the Indonesian-German research project STORMA (Stability of Rainforest Margins in Indonesia, SFB 552; http://www.uni-goettingen.de/de/sh/40515.html). Bats were surveyed in the following four habitat types (N = 4 sites per habitat): (A) natural forest, (C) selectively logged forest, (D) agroforestry systems with a diverse layer of shade trees remaining from the formerly logged natural forest and (F) agroforestry systems with a homogeneous shade tree layer consisting of only one planted tree species. Habitat abbreviations (A, C, D, F) correspond to habitat codes also used by other STORMA research projects. The 16 study sites are situated at an altitude between 799 and 1130 m asl and represent plots of 0.16 ha (40 x 40 m) in size. The spatial distribution of the plots within the study area is shown in Figure 1, coordinates and altitudes of all plots are provided in Table A (Appendix).

Several biotic (e.g. vegetation structure and diversity) and abiotic habitat variables (e.g. microclimate) already measured in the framework of other research activities (e.g. Wanger *et al.* 2010) were available for our study. We used the

following four habitat variables (see Appendix Table B) and related them to bat richness and the occurrence of individual species: (1) canopy closure, (2) shrub density, (3) shrub height and (4) number of larger trees with a diameter at breast height (dbh) of more than 50 cm per plot. The first three habitat variables were measured in all four corners and the middle of the plots. Then we calculated the mean of each parameter from all five locations. To determine the percentage of canopy cover, 180° photographs of the canopy were taken using a fisheye lens setting up the camera (Canon Powershot, 5 megapixels) on a 1.70 m tripod and pointing it directly towards the sky. Pictures were then evaluated using the ImageJ software (Rasband 2008). Shrub height was estimated as the average height of 10 representative plants; shrub density was quantified as the mean number of plants in 50 x 50 cm squares (Wanger *et al.* 2010).

Sampling

Bats were caught between 22 August 2008 and 5 November 2008 with ground mist nets (12 m x 2.5 m, 30 mm mesh) (e.g. Pineda *et al.* 2005). Disturbance of the understorey vegetation may alarm bats patrolling familiar territory. To minimize this disturbance, the nets were set along existing trails or vegetation structures. However, some clearing was necessary to avoid the nets entangling with the vegetation and to leave enough space to work on each side of the nets (e.g. Simmons and Voss 1998). Mist netting was conducted on two consecutive days per site using four mist nets simultaneously. The four mist nests were set to cover as much area of the plot as possible.

On each sampling night the mist nets were operated for 6 h after sunset (6 pm-12 pm) (e.g. Simmons and Voss 1998, Bernard and Fenton 2002), conditioned by weather (no heavy rain), and were checked every 30 minutes. In case of heavy rain, sometimes mist nests were closed earlier to avoid a potentially increased mortality of trapped bats. Once captured, each bat was identified, weighed, sexed and measured (body, forearm, ear, tail and tarsus length). Afterwards they were released at the site of capture. To avoid pseudo-replication, they were marked with individual numbers written on their wings with a permanent marker.
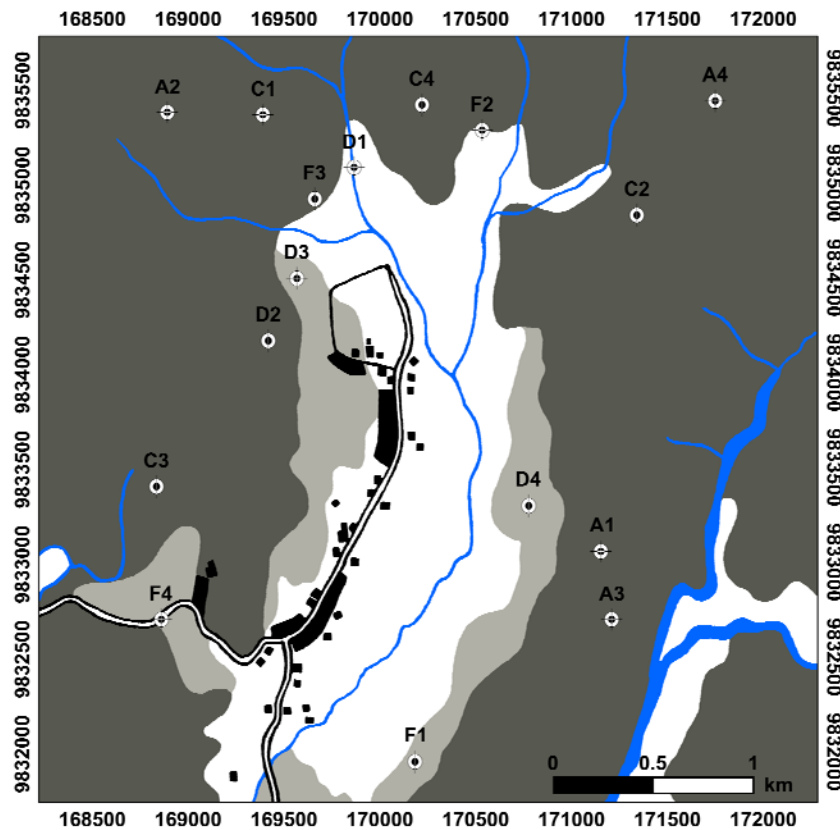
Figure 1 Schematic map of the study area showing the spatial distribution of the four study sites of each habitat type (A = natural forest, C = selectively logged forest, D = agroforestry systems with a diverse layer of shade trees remaining from the formerly logged natural forest, F = agroforestry systems with a homogeneous shade tree layer consisting of only one planted tree species). Different colors indicate habitat types: settlements (black), water bodies (blue), openland (white), forest and agroforestry systems (grey shades).

Bat identification

A local field assistant experienced in mist netting of bats and familiar with the local bat fauna was available to assist in bat identification. Additionally, identification keys (Payne *et al.* 1985, Suyanto 2001, Francis 2008, Srinivasulu *et al.* 2010, The Nature Conservancy unpublished) were used. Photographs of characteristic morphological structures and color patterns were taken to ensure the identifications afterwards.

Data analysis

Capture rate calculated as the number of individuals caught per net-meter-hour (meaning one meter net open for one hour) was used as abundance measure (e.g. Aguirre 2002). Effects of habitat types (A, C, D and F) on species richness and abundance were tested by one-way ANOVAs. Subsequent post-hoc tests were

carried out using Tukey's honestly significantly different (HSD) tests. We used generalized linear models (GMLs) and Spearman's rank correlations to test for effects of habitat variables on abundances. When multiple univariate tests were used to relate various habitat variables to changes in bat abundance, a Bonferroni correction was applied.

To evaluate the completeness of the recorded species assemblage, species accumulation curves based on Mao-Tau function were generated. Total expected species richness was estimated using EstimateS 7.5.2 (Colwell 2005) by randomizing samples 50 times. Referring to Walther and Moore (2005) Chao 2 richness estimator (Chao2) and Second-order Jackknife richness estimator (Jack2) were used to estimate species richness because they usually provide the most reliable estimates. Using square-root transformed abundance data, species composition was quantified by Bray-Curtis similarity indices calculated by PRIMER 5.2.9 (Clarke and Gorley 2001). Furthermore, species assemblages were tested for nestedness with BINMATNEST (Rodríguez-Gironés and Santamaría 2006). Therefore, system temperatures of presence-absence matrices were compared with the average temperature of 1,000 randomized matrices. For running the calculation recommended programm setting were used (see instructions provided by BINMATNEST; Rodríguez-Gironés and Santamaría 2006). When not mentioned otherwise, all other analyses were performed using Statistica 7.1 (StatSoft 2005).

Results

Species richness and abundance

In total, 195 bats (not including 3 recaptures) belonging to 5 families, 8 genera and 13 species (Table 1) were caught during 8592 net-meter-hours. Of these, 106 bats were caught at F sites, 80 at D sites, 3 at C sites and 6 at A sites. A total of 8 bats managed to escape before being identified to species level and therefore were excluded from further analysis of diversity. Overall capture rate was 0.023 bats per net-meter-hour. The three most common species *Rousettus amplexicaudatus*, *Cynopterus brachyotis* and *C. sphinx* made up 73.3% of the total individuals and were found in both forests and agroforestry systems (Table 1). The entire species

assemblage was dominated by macrochiropteran bats, which represented 95.2% of all individuals (Table 1).

In total 4, 1, 11 and 7 species were caught at A, C, D and F sites, respectively. The number of species recorded per site was significantly affected by habitat type (one-way ANOVA: $F_{3,12}$ = 45.07, p < 0.001). The mean number of bat species recorded per site was significantly lower in the two forest habitats A and C than in the two agroforestry systems D and F (Fig. 2a). Also, the number of individuals caught per net-meter-hour was significantly affected by habitat type (one-way ANOVA: $F_{3,12}$ = 6.78, p = 0.006). Highest numbers of bats were found in F, the smallest numbers were recorded in both forest types A and C. Intermediate abundances, which did not differ significantly from habitat types A, C and D, were recorded for the agroforestry system D (Fig. 2b).

Table 1   Number of understorey bat individuals per species caught in two different forest types (A, C) and two different agroforestry systems (D, F) in Central Sulawesi, Indonesia

Order/Family	Species	A	C	D	F	Total
Macrochiroptera						
Pteropodidae	*Macroglossus minimus* (Geoffroy, 1810)	0	0	4	13	17
	Cynopterus brachyotis (Müller, 1838)	1	0	20	29	50
	Cynopterus sphinx (Vahl, 1797)	1	0	14	15	30
	Cynopterus sp.	0	0	1	0	1
	Rousettus amplexicaudatus (Geoffroy, 1810)	0	3	20	40	63
	Rousettus celebensis (Andersen, 1907)	0	0	10	5	15
	Rousettus sp.	1	0	3	2	6
	Thoopterus nigrescens (Gray, 1870)	2	0	1	0	3
Microchiroptera						
Rhinolophidae	*Rhinolophus borneensis* (Peters, 1861)	1	0	0	0	1
	Rhinolophus euryotis (Temminck, 1835)	0	0	1	0	1
Hipposideridae	*Hipposideros cervinus* (Gould, 1863)	0	0	1	0	1
Verspertilionidae	*Myotis ater* (Peters, 1866)	0	0	1	0	1
	Myotis horsfieldii (Temminck, 1840)	0	0	0	1	1
	Myotis muricola (Gray, 1864)	0	0	1	1	2
Megadermatidae	*Megaderma spasma* (Linnaeus, 1758)	0	0	2	0	2
unknown	unknown	0	0	1	0	1
Total		6	3	80	106	195

A = natural forest, C = selectively logged forest, D = agroforestry systems with a diverse layer of shade trees remaining from the formerly logged natural forest, F = agroforestry systems with a homogeneous shade tree layer consisting of only one planted tree species.
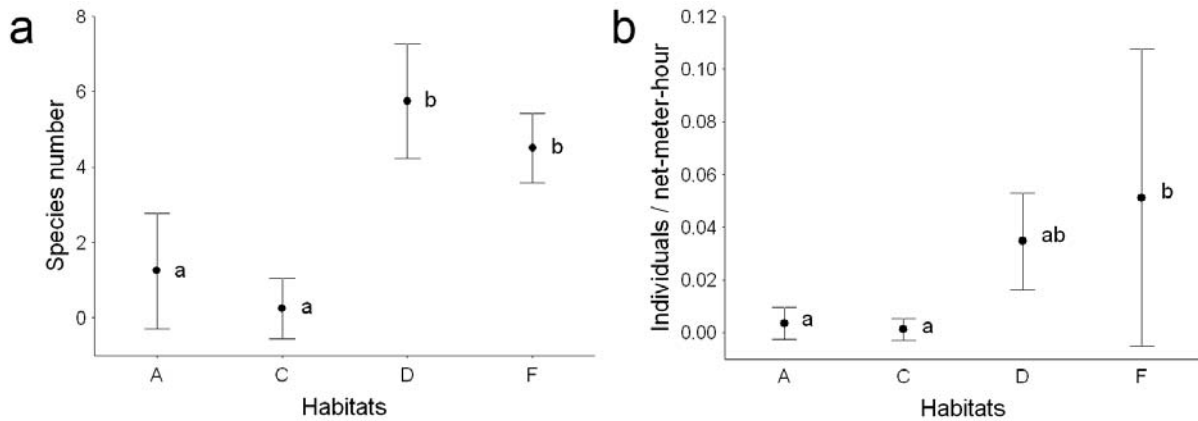
Figure 2 Mean number (± 95% CI) of (**a**) observed species and (**b**) individuals (caught per net-meter-hour) per site in each habitat type (A = natural forest, C = selectively logged forest, D = agroforestry systems with a diverse layer of shade trees remaining from the formerly logged natural forest, F = agroforestry systems with a homogeneous shade tree layer consisting of only one planted tree species). Different letters indicate differences at $p < 0.05$ (Tukey´s HSD test).

Due to the low capture rates of bats in the two forest habitats they were pooled for analysis of species richness. Species accumulation curves (Mao-Tao function) indicate highest species richness for forest and agroforestry system D (Fig. 3). However, the accumulation curve for the two forest types has to be interpreted with caution due to the small number of individuals caught at forest sites (only total of 9 individuals). Furthermore, the shape of the curves for A+C and D plots indicate that inventories of bat species assemblages are still rather incomplete. According to the 95% CIs of the species accumulation curves for the habitat types D and F, bat species richness was significantly higher in agroforestry system D (Appendix Figure A).
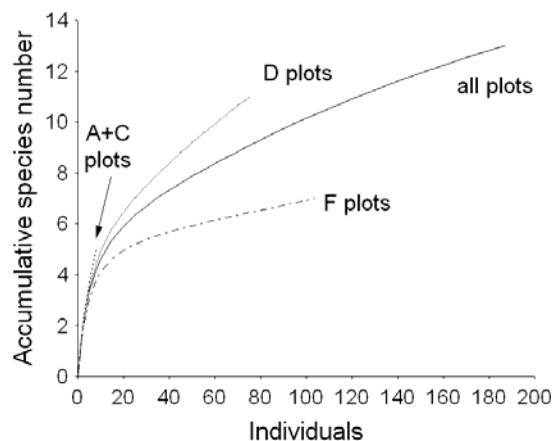

Figure 3 Species accumulation curves (based on Mao-Tau function) for all plots, F plots, D plots and A+C plots (pooled). A = natural forest, C = selectively logged forest, D = agroforestry systems with a diverse layer of shade trees remaining from the formerly logged natural forest, F = agroforestry systems with a homogeneous shade tree layer consisting of only one planted tree species.

Higher species richness in agroforestry system D compared to F was supported by the Chao2 and Jack2 richness estimates (Table 2). As already indicated by the shape of the species accumulation curves, also both richness estimators indicate low completeness of recorded species inventories, particularly for forest sites and D plots (Table 2). However, again results for the forest plots have to be interpreted with caution due to their small sample sizes.

Table 2 Total number of individuals, recorded species, species richness and completeness of species inventories estimated by Chao2 and Jack2 for forest A+C (plots pooled) and the two agroforestry systems D and F.

Habitats	Individuals	Species	Estimates		Completeness [%]	
			Jack2	Chao2	Jack2	Chao2
A+C plots	8	5	10.47	7.5	47.8	66.7
D plots	75	11	19.71	15.88	55.8	69.3
F plots	104	7	10.87	7.98	64.4	87.7
all plots	187	13	20.9	16.3	62.2	79.8

Habitats: A = natural forest, C = selectively logged forest, D = agroforestry systems with a diverse layer of shade trees remaining from the formerly logged natural forest, F = agroforestry systems with a homogeneous shade tree layer consisting of only one planted tree species; richness estimators: Jack2 = Second-order Jackknife richness estimator, Chao2 = Chao 2 richness estimator.

Species composition

Species composition (quantified by Bray-Curtis similarities using square-root transformed abundance data) did not differ between the two agroforestry systems D and F (one-way ANOSIM: global r = -0.08, p = 0.714). However, the occurrence of bat species at individual sites was not random, but proved to be nested (BINMATNEST: matrix T = 13.22, p = 0.015; Fig. 4).
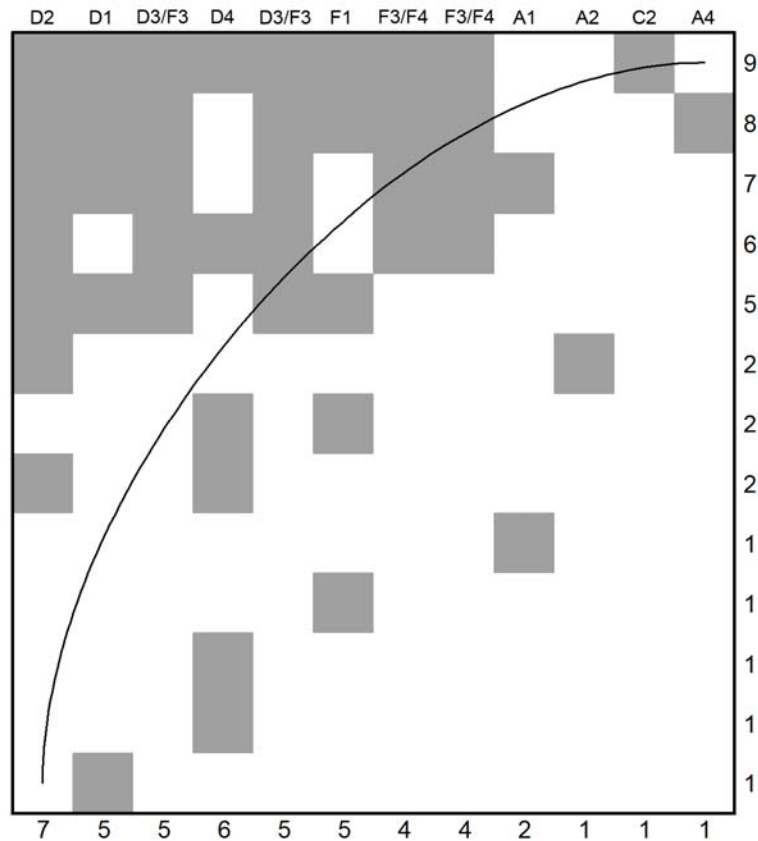
Figure 4 Presence-absence matrix of understorey bat species recorded at forest and agroforestry system plots packed into the state of maximum nestedness. The curve indicates the boundary for a perfectly sorted matrix and unexpected species occurrences are shown below. Numbers represent total number of recorded species per site (columns) and total number of sites from which individual species were recorded (rows). Results of the test for nestedness (BINMATNEST): matrix T = 13.22, p = 0.015. Codes at the top margin of the graph represent plot abbreviations (A = natural forest, C = selectively logged forest, D = agroforestry systems with a diverse layer of shade trees remaining from the formerly logged natural forest, F = agroforestry systems with a homogeneous shade tree layer consisting of only one planted tree species).

Habitat preferences and effects of vegetation structure

One-way ANOVAs were calculated to test for differences of habitat variables between the four habitat types. Mean canopy closure and the number of tall trees (dbh >50 cm) differed significantly between habitats (canopy closure: $F_{3,12}$ = 18.67, p < 0.001; tall trees: $F_{3,12}$ = 5.03, p = 0.017). Mean canopy closure was significantly lower in agroforestry system F compared to the three other habitat types (Fig. 5a). The number of tall trees was significantly higher in natural forest compared to the two agroforestry systems. Selectively logged forest was intermediate (Fig. 5b). No differences between habitat types were indicated for shrub density ($F_{3,12}$ = 0.47, p = 0.708) and shrub height ($F_{3,12}$ = 1.63, p = 0.233).
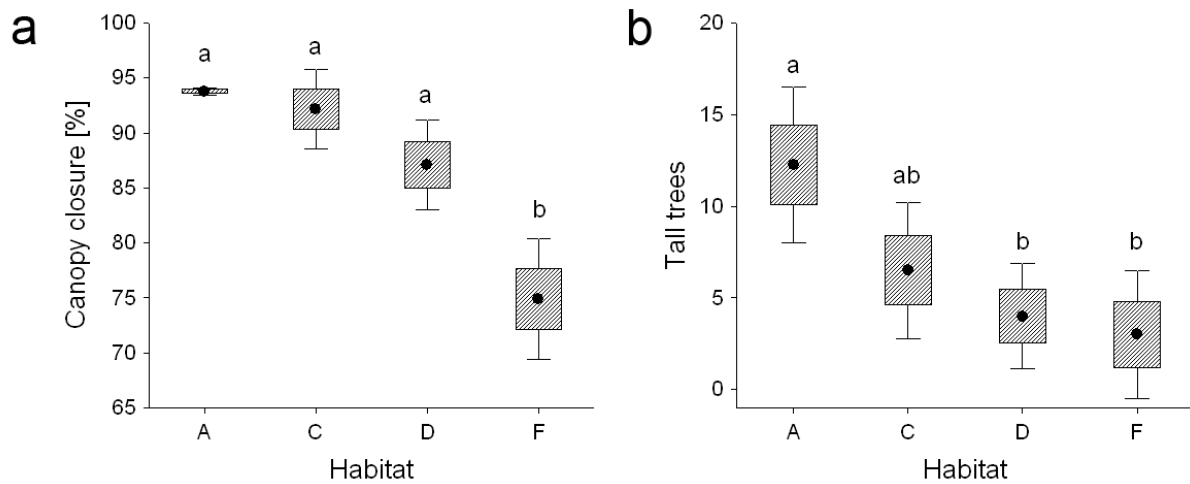
Figure 5 (**a**) Mean canopy closure [%] and (**b**) number of tall trees per plot ± SE (box) and SD (whiskers) of natural forest (A), selectively logged forest (C), agroforestry systems with a diverse layer of shade trees remaining from the formerly logged natural forest (D) and agroforestry systems with a homogeneous shade tree layer consisting of only one planted tree species (F). Different letters indicate significant differences (Tukey's HSD test; $p < 0.05$).

GLMs were calculated to test for effects of mean canopy closure, mean shrub density, mean shrub height and number of tall trees (dbh >50cm) on species richness and individuals caught per net-meter-hour. Although the GLM testing for effects on bat species richness achieved a significant level ($r_{multiple} = 0.75$, $r^2_{multiple} = 0.56$, $F_{4,11} = 3.63$, $p = 0.040$), it did not indicate a significant effect for an individual variable. The GLM testing for effects on bat abundance was not significant ($r_{multiple} = 0.65$, $r^2_{multiple} = 0.43$, $F_{4,11} = 2.04$, $p = 0.157$).

To identify habitat preferences of bat species, abundances per plot were compared between habitats, only considering species with more than 10 captures (N = 5 species). Kruskal-Wallis one-way analyses of variance indicate a significant effect for all species (all p values < 0.05), but this may only be caused by the generally low capture rates at A and C plots. For all 5 species no significant differences between the two agroforestry systems could be recorded (Mann-Whitney U-tests: all p values > 0.05). Spearman's rank correlations were used to relate the abundances of these species with each of the four measured habitat variables. After Bonferroni correction, three correlations remained significant: the abundance of *Cynopterus brachyotis* and *Rousettus amplexicaudatus* was negatively related to canopy closure, and the abundance of *Rousettus celebensis* decreased significantly with an increasing number of tall trees (see Table 3).

Table 3 Results of Spearman rank correlations testing for relationships between mean canopy closure, mean shrub density, mean shrub height and number of tall trees (dbh > 50 cm) per plot on abundances (individuals caught per net-meter-hour) of the five most abundant bat species (>10 captures). Provided are correlation coefficients and *p* values (in parentheses). Relationships which remained significant after Bonferroni correction are printed in bold.

| Species | Habitat variables | | | |
	Canopy closure	Shrub density	Shrub height	Trees
Macroglossus minimus	-0.565 (0.023)	0.220 (0.413)	-0.375 (0.152)	-0.404 (0.120)
Cynopterus brachyotis	**-0.638 (0.008)**	0.033 (0.903)	-0.335 (0.205)	-0.547 (0.028)
Cynopterus sphinx	-0.425 (0.101)	0.047 (0.862)	-0.203 (0.451)	-0.417 (0.108)
Rousettus amplexicaudatus	**-0.745 (<0.001)**	0.241 (0.368)	-0.313 (0.237)	-0.575 (0.020)
Rousettus celebensis	-0.449 (0.081)	-0.266 (0.319)	-0.562 (0.023)	**-0.671 (0.004)**

Discussion

Abstract and species richness

Abundance and species richness

With 195 individuals trapped during 8,592 net-meter-hours we achieved an overall capture rate of 0.023 bats per net-meter-hour. Similar capture rates of 0.021 (7,333 bats during 346,500 net-meter-hours; Sampaio *et al.* 2003) and 0.054 individuals per net-meter-hour (3,978 bats during 73,392 net-meter-hours; Bernard and Fenton 2002) were found by studies using ground mist nets to assess bat communities in Brazil. Only rarely much higher capture rates of 0.098 individuals per net-meter-hour (2,444 bats during 24,957 net-meter-hours) were achieved such as by a study in French Guiana (Simmons and Voss 1998). However, this notably higher capture rate may have been caused by a modified mist netting method additionally attracting bats using high-pitched squeaks resembling the distress calls of Stenodermatinae bats (Simmons and Voss 1998).

According to Whitten *et al.* (2002) the total number of bat species recorded for Sulawesi is about 62 with 17.5% endemism, not including a just recently described *Hipposideros* species (Bates *et al.* 2007). Significantly more species (91) are recorded on neighboring Borneo (Payne *et al.* 1985), while a similar number of bats (68 species) occur in Java (Whitten *et al.* 2000). A total number of 13 bat species was recorded from our study area at the western margin of Lore Lindu National Park in Central Sulawesi and a total of 16 and 21 species were estimated by the richness

estimators Chao2 and Jack2, respectively. During 32 harp-trap nights in the lowlands of Rawa Aopa Watumohai National Park, South-east Sulawesi a total of 84 individuals belonging to 8 species were caught. When applying rarefaction to our species accumulation curve for all 16 study sites a very similar number of ca. 9 bat species is expected for an identical sample size of 84 individual. This emphasizes the low local species richness of bat assemblages in Sulawesi compared to studies from other locations in the Oriental region. Studies from Vietnam and Borneo recorded 36 (Furey *et al.* 2010) and 28 (Fukuda *et al.* 2009) bat species, respectively.

In this study, bats were sampled using ground mist nets, which are commonly used for bat surveys and are by far the most effective method for recording a large fraction of the species assemblage in an area (Voss and Emmons 1996). A problem arising from mist netting exclusively at ground level is that it does not sample species restricted to the canopy. However, in a Malaysian lowland forest most of the bat species were captured throughout the vertical forest profile. Only one species had a capture rate varying significantly between vegetation strata, showing a strong preference for the understorey (Hodgkison *et al.* 2004). Also a mist net study from the Southern Amazon found only few species exclusively flying in the canopy (Peters *et al.* 2006). Additionally, species with a main flight activity during the second half of the night may be underrepresented in our study because we only conducted mist netting from 6 pm to 12 pm. However, all studies on nocturnal flight activity of bats recorded an activity peak in the first hours after dusk for almost all species and activity generally declined throughout the night (e.g. Kunz and Brock 1975, Simmons and Voss 1998, O'Donnell 2000, Milne *et al.* 2005). Therefore, the low estimated completeness of our species inventory may be predominately caused by the difficulty of assessing tropical bat assemblages containing many rare species and not by a bad coverage of the vertical and temporal activity patterns of bats in forest and agroforestry habitats.

Both the species accumulation curve and species richness estimators indicated a relatively high incompleteness of our species inventory. The richness estimators Jack2 and Chao2 estimated that between 62.2% and 79.8% of the expected number of species were recorded during 8,592 net-meter-hours. Other mist net studies from Brazil, French Guiana and Mexico achieved a higher completeness

of 86-97%, 91% and 90% of the expected total species number but with a much higher sampling effort of 346,500 (Sampaio *et al.* 2003), 24,957 (Simmons and Voss 1998) and 26,996 (Moreno and Halffter 2000) net-meter-hours, respectively. Only a study from Brazil by Bernard and Fenton (2002) reached a similar completeness of 67-89% although the sampling effort was much higher (73,392 net-meter-hours) than in our study (8,592 net-meter-hours). In all these studies a large proportion of the local bat fauna was recorded during the first sampling sessions and less common species accumulated successively in the later stages. In most bat inventories the majority of species are captured within 30 nights (our study: 32 nights), in about 12,000 net-meter-hours or with a capture effort of at least 1,000 individuals. The increase of the species accumulation normally slows down after reaching about 70% of the total number of species in a certain location. Then an intensified capture effort or additional survey methods are needed to go beyond the common species and to include rarer species (Sampaio *et al.* 2003). Notably aerial insectivores are typically underrepresented or completely missing in species inventories achieved by the exclusive use of mist nets because bats of this feeding guild forage mainly in spaces which are difficult or even impossible to sample with mist nets (Voss and Emmons 1996, Simmons and Voss 1998). Only through the use of other methods such as the identification of aerial insectivores by their echolocation calls the effectiveness of bat surveys can be increased (Kuenzi and Morrison 1998, O'Farrell and Gannon 1999, Sampaio *et al.* 2003).

Species composition

As indicated by calculated Bray-Curtis similarities, the species composition of the two different cacao agroforestry systems sampled in our study did not differ. Due to small sample sizes no reliable Bray-Curtis similarities could be calculated for the two forest sites. However, our test for nestedness of species assemblages of all 16 plots indicates that forest sites may not be characterized by a distinct species composition but their species assemblages may rather represent subsets of more diverse communities recorded in agroforestry systems. By contrast, a study of bird species composition differed clearly between the four habitat types (Waltert *et al.* 2004).

Habitat preferences and vegetation structure

Habitat structure may have an important influence on the presence of understorey bats due to their limited maneuverability in dense understorey. The maneuverability of bats is mainly achieved as a result of body size and wing-load. While short and broad wings enable a slow, maneuverable flight, allowing bats to fly within the vegetation, long and slender wings, on the other hand, enable a fast flight suitable for open spaces (Norberg and Rayner 1987, Neuweiler 1993, Stockwell 2001). As bats often move on flight paths along present vegetation structure, such as hedgerows or habitat edges (Racey and Swift 1985, Verboom and Huitema 1997, Wickramasinghe *et al.* 2003), dense thicket has the potential to impede the flight of bats (Norberg and Rayner 1987, Kalko *et al.* 1996a). At our study sites vegetation density changed from the ground level to the upper canopy in a habitat-specific pattern. At forest sites highest vegetation density was found in the understorey (up to 5 m). The mid-storey (5 m to 20 m) was relatively open, whereas vegetation density increased again in the canopy (20-30 m). Agroforestry systems, by contrast, were generally open spaced as a result of shade tree management and additionally potential flight corridors existed at ground level below the cacao scrub canopies. It is therefore not surprising that we recorded higher abundances of bats in the understorey of cacao agroforestry systems than in forests. However, bats at forest sites may have used higher strata with lower vegetation densities (e.g. mid-storey layer) better suited to their specific maneuverability. Consequently, they may have not been sampled effectively by our ground mist nets.

The much higher abundances of frugivorous macrochiropteran bats at agroforest sites may be caused by an easier detection of fruits. Macrochiropteran bats generally have large, light sensitive eyes, and sight appears to be their major navigating sense (Neuweiler 1993). Thus more open spaced woody habitats such as agroforestry systems may represent a preferred feeding habitat for frugivorous forest bats.

Increasing canopy closure caused decreasing abundances of *Cynopterus brachyotis* and *Rousettus amplexicaudatus*, all other species had at least a tendency to decline. *Rousettus celebensis* was furthermore negatively affected by the number of tall trees with diameter at breast height of more than 50 cm. It is therefore not

surprising, that agroforestry systems maintained bat assemblages with higher species richness, abundance and diversity as forests. Harvey and González Villalobos (2007) found similar results in the Neotropics, recording a basic suite of dominant species in both forests and land-use systems, but more frugivorous and nectarivorous bats in agroforestry systems.

Although our study recorded only a few bats caught with mist nets in the two forest habitats, a substantial number of flying individuals could be observed. Bats can change the structure of echolocation calls to adapt to specific circumstances. The repertoire ranges from long calls of small bandwidth with long pulse intervals, usually used in open space, to short broadband calls with short pulse intervals, normally used close to vegetation due to the greater performance in resolution of the environment (Siemers and Schnitzler 2000, Jones and Holderied 2007). The percentage of caught microchiropteran bats in general was remarkably low, indicating that they may have noticed the mist nets by using echolocation. To minimize this bias it is recommended to use harp traps in addition to mist nets since they return lower echoes and are consequently more effective in trapping echolocating bats (e.g. Berry *et al.* 2004). Nevertheless, some microchiropteran bats were caught on agroforest plots. Most likely they flew on familiar flight paths and only infrequently used echolocation, and therefore were caught only by chance. Due to the extremely dense vegetation of the forest understorey flying Microchiroptera individuals may more continuously use their echolocation and thereby detect and avoid mist nets.

Food availability

Frugivorous bats usually carry fruits in their mouth to a nearby temporary dining roost (Kalko *et al.* 1996b). In our study several bats were caught still carrying fig fruits (1x *Cynopterus* species) and the infructescences of *Piper aduncum* (individuals of several species) in their mouth. Additionally, the seeds of *Piper aduncum* (Piperaceae) were noticed in the excrement of the majority of caught bats. Even the excrements of *Macroglossus minimus*, a species characterized as primarily feeding on nectar and pollen (e.g. from banana *Musa*, coconut *Cocos nucifera*, mangrove trees of family Sonneratiaceae; Gunnell *et al.* 1996) contained seeds of *Piper*

aduncum. Remarkably, no significant pollen loads, indicating that these individuals recently visited flowers, were found on the heads of captured *Macroglossus minimus* individuals (S. Graf, unpublished). As many frugivorous bats forage for fruits and flowers (e.g. Hodgkison and Balding 2004) most caught bats were examined for pollen attached to their fur to identify potential food sources. However, not a single specimen was trapped carrying an amount of pollen which would have indicated a recent flower visit (S. Graf, unpublished).

Many South-east Asian bats appear to be food generalists (Fleming and Muchhala 2008) opportunistically exploiting available and easily accessible food sources. Although we did not measure food availability, it appeared to be lower in the forest than in cacao agroforests. Whereas no considerable food sources for bats have been noticed on our forest plots, *Piper aduncum*, recorded as an important food source in our study, was very abundant along the edges of the sampled cacao plantations. *Piper aduncum* is an invasive shrub growing abundantly at disturbed sites in human-dominated habitats (Ramadhanil *et al.* 2008). Furthermore, occasionally fruit trees (e.g. *Ficus* sp.) can be found on the plots. Particularly fig fruits are important 'keystone' food sources for many frugivorous animals, including bats (Kalko *et al.* 1996b). Although only one bat carrying a fig fruit in its mouth was trapped during our study, bats were frequently observed visiting fig trees at our agroforest plots. To summarize, in our study area both *Piper aduncum* and *Ficus* fruits may represent the most important food source for frugivorous bats. Their high availability inside (*Ficus*) or at the margin of agroforestry systems (*Piper aduncum*) may be prime factor explaining the high abundances of bats at our D and F agroforest plots.

Implications for conservation

Bats are highly mobile animals with the ability to cover several kilometers during a single night (e.g. Racey and Swift 1985, Verboom and Huitema 1997, Wickramasinghe *et al.* 2003) exploring huge feeding areas and may use certain agroforestry systems only temporarily during foraging (Pineda *et al.* 2005). The occurrence of bats in our study area may therefore heavily depend on both the habitat matrix at the margin of Lore Lindu National Park and the local food availability. Higher bat abundances in D plots representing agroforestry systems

mostly embedded in the forest margin may indicate the importance of adjacent forest perhaps providing necessary daytime roosting sites. The potential of agroforestry systems to contribute to bat species richness may therefore be closely linked to the existence of nearby forests acting as sources areas. Previous studies on community structure of various animal groups, including frogs and lizards (Faria *et al.* 2007), birds (Greenberg *et al.* 2000) and bats (Faria and Baumgarten 2007, Cassano *et al.* 2009) led to similar conclusions.

Therefore, our results have to be interpreted with great caution and do not allow for the conclusion that forests can be replaced by any kind of agro-ecosystems in terms of bat conservation. Forest bats are often very sensitive to forest modification (e.g. Gorresen and Willig 2004, Armbrecht *et al.* 2005, Medellín *et al.* 2008) and these species may have been insufficiently recorded by our mist netting study. However, our data did indicate that land-use systems such as agroforestry systems with a diverse layer of shade trees remaining from the formerly logged natural forest can support relatively high numbers of bats visiting them in the context of foraging. Therefore, they might play a significant role as buffer zone habitats around forest remnants embedded in nowadays predominately human-dominated tropical landscapes (for similar findings see Faria and Baumgarten 2007, Harvey and González Villalobos 2007). To assess the actual value of agroforestry systems as buffer zone habitats for bats at the margin of forest reserves, further studies have to focus on quantifying the habitat requirements of forest-dwelling bat species.

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Appendix

Table A
Geographical position and elevation of the 16 study plots in Central Sulawesi, Indonesia

Habitat type	Site code	UTM X 51S (m)	UTM Y 51S (m)	Elevation (m asl)
A	A1	171125	9832974	948
	A2	168961	9835116	1130
	A3	171204	9832688	955
	A4	171759	9834927	1018
C	C1	169292	9834866	974
	C2	171334	9834440	878
	C3	168716	9833262	827
	C4	170165	9834914	959
D	D1	169787	9834639	837
	D2	169333	9833896	952
	D3	169489	9834158	832
	D4	170737	9833172	806
F	F1	170125	9832058	801
	F2	170485	9834798	825
	F3	169577	9834508	833
	F4	168735	9832676	799

A = natural forest, C = selectively logged forest, D = agroforestry systems with a diverse layer of shade trees remaining from the formerly logged natural forest, F = agroforestry systems with a homogeneous shade tree layer consisting of only one planted tree species

Table B
Habitat parameters (see supplementary material Wagner *et al.* 2010) used for analysis on effects of vegetation structure

Habitat type	Site code	CC	SD	SH	LOGS
A	A1	94.2	3.0	140	8
	A2	93.7	4.8	185	13
	A3	93.9	1.0	57	18
	A4	93.4	3.6	110	10
C	C1	86.8	3.4	120	4
	C2	94.0	5.0	130	6
	C3	95.0	3.6	67	4
	C4	93.0	3.2	127	12
D	D1	84.0	4.4	128	5
	D2	88.7	4.8	65	0
	D3	92.3	2.4	10	4
	D4	83.5	4.8	60	7
F	F1	71.5	2.2	33	0
	F2	72.0	3.4	10	0
	F3	72.8	5.0	70	7
	F4	83.3	4.6	139	5

Habitat types: A = natural forest, C = selectively logged forest, D = agroforestry systems with a diverse layer of shade trees remaining from the formerly logged natural forest, F = agroforestry systems with a homogeneous shade tree layer consisting of only one planted tree species; Habitat variables: CC = mean canopy closure [%], SD = mean shrub density [1-5], SH = mean shrub height [cm], LOGS = number of tall trees (DBH ≥50 cm)
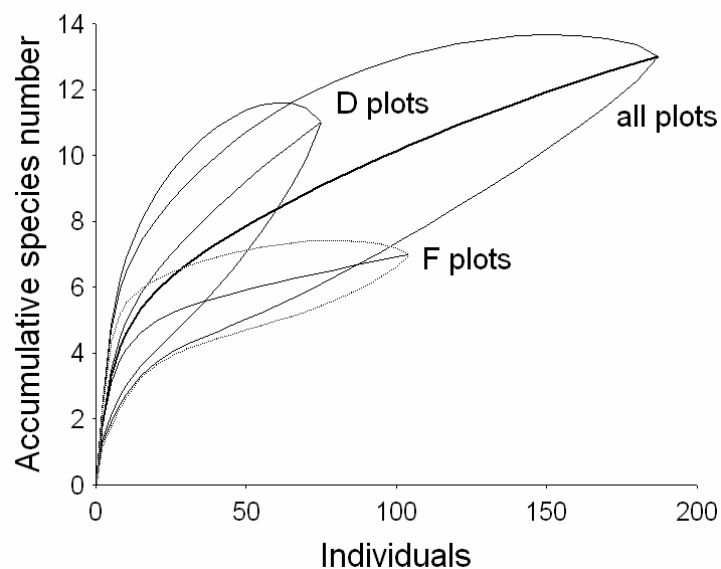

Figure A   Species accumulation curves (based on Mao-Tau function) ± 95% CI for all plots, F plots and D plots. D = agroforestry systems with a diverse layer of shade trees remaining from the formerly logged natural forest, F = agroforestry systems with a homogeneous shade tree layer consisting of only one planted tree species.

Curriculum Vita

Name: Stefan Graf
Address: A-1040 Vienna, Schelleingasse 14-16/3/7
e-mail: a0009941@unet.univie.ac.at
Place of birth: Vienna, Austria
Date of birth: 4th April 1981
Nationality: Austrian

08/2008 – 11/2010	Diploma thesis at the Department of Animal Biodiversity, University of Vienna.
	"Diversity and habitat use of understorey bats in forest and agroforestry systems at the margin of Lore Lindu National Park (Central Sulawesi, Indonesia)", with field work in Central Sulawesi, Indonesia (08/2008 – 11/2008)
10/2000 – 11/2010	Study of Biology at University of Vienna (Austria)
	with main subject zoology (since February 26, 2003)
10/1999 – 05/2000	Military service
09/1991 – 06/1999	High school: „Neulandschule"
	Ludwig von Höhnel Gasse 17-19, A-1100 Vienna, Austria
09/1987 – 06/1991	Elementary school: „Neulandschule"
	Ludwig von Höhnel Gasse 17-19, A-1100 Vienna, Austria

Language Skills

German … native language
English … good skills, written and spoken