Alpha and beta diversity of plants and animals along a tropical land-use gradient

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Abstract. Assessing the overall biological diversity of tropical rain forests is a seemingly insurmountable task for ecologists. Therefore, researchers frequently sample selected taxa that they believe reflect general biodiversity patterns. Usually, these studies focus on the congruence of α diversity (the number of species found per sampling unit) between taxa rather than on β diversity (turnover of species assemblages between sampling units). Such approaches ignore the potential role of habitat heterogeneity that, depending on the taxonomic group considered, can greatly enhance β diversity at local and landscape scales. We compared α and β diversity of four plant groups (trees, lianas, terrestrial herbs, epiphytic liverworts) and eight animal groups (birds, butterflies, lower canopy ants, lower canopy beetles, dung beetles, bees, wasps, and the parasitoids of the latter two) at 15 sites in Sulawesi, Indonesia, that represented natural rain forest and three types of cacao agroforests differing in management intensity. In total, we recorded 863 species. Patterns of species richness per study site varied strongly between taxonomic groups. Only 13–17% of the variance in species richness of one taxonomic group could be predicted from the species richness of another, and on average 12–18% of the variance of β diversity of a given group was predicted by that in other groups, although some taxon pairs had higher values (up to 76% for wasps and their parasitoids). The degree of congruence of patterns of α diversity was not influenced by sampling completeness, whereas the indicator value for β diversity improved when using a similarity index that accounts for incomplete sampling. The indication potential of α diversity for β diversity and vice versa was limited within taxa (7–20%) and virtually nil between them (0–4%). We conclude that different taxa can have largely independent patterns of α diversity and that patterns of β diversity can be more congruent. Thus, conservation plans on a landscape scale need to put more emphasis on the high heterogeneity of agroforests and the overarching role of β diversity shaping overall diversity patterns.

Key words: agroforests; biodiversity indication; community similarity; indicator species; Indonesia; species richness; Sulawesi, Indonesia; tropical rain forest.

INTRODUCTION

The immense diversity of tropical plant and animal communities faces ever-increasing risk of extinction (e.g., Jetz et al. 2007), but our inadequate taxonomic knowledge of tropical taxa continues to limit the scope and extent of biodiversity assessments. Accordingly, researchers frequently employ selected surrogate taxa believed to reflect overall levels of biodiversity (Pearson 1994, Prendergast 1997, Phar et al. 1999, Rodrigues and Brooks 2007). Such surrogate taxa can be flagship species (chosen for their charisma), focal taxa (individual species of particular conservation concern), keystone species (with high ecological impact), umbrella species (requiring large areas of habitat, thereby providing space for other taxa), or indicator taxa (with the same habitat requirements as the species or communities that they indicate) (e.g., Paine 1969, Wilcox 1984, Landres et al. 1988, Mittermeier 1988, Lambeck 1997, Simberloff...
Moreover, a larger spatial scale is made up of (Cody 1986, Crist et al. 2003). Most of the diversity at site or spatial level to another (Whittaker 1960, 1972, derived from changes in species composition from one richness at a given site or spatial level and distinction is between (Whittaker 1960, 1972, Hubbell 2001). The classical distinction is between α diversity derived from species richness at a given site or spatial level and β diversity derived from changes in species composition from one site or spatial level to another (Whittaker 1960, 1972, Cody 1986, Crist et al. 2003). Most of the diversity at larger spatial scales is made up of β diversity (Crist et al. 2003, Crist and Veech 2006, Gabriel et al. 2006). Moreover, α and β diversity may reveal contrasting spatiotemporal patterns (Tylianakis et al. 2005), and the extent to which α diversity can predict β diversity can differ between taxonomic groups. Hence, comparing α and β diversity at local and landscape scales is an important yet little-understood area of basic and applied ecological research.

Although the basic conceptual distinction between α and β diversity is well established in the ecological literature, the analytical problems that arise from this distinction are complex and not yet fully explored, especially in the context of biodiversity conservation. First, levels of diversity can be measured at different spatial scales, which may require partitioning of the diversity (Whittaker 1960, 1972, Crist et al. 2003, Crist and Veech 2006). Second, a fundamental complication arises from the fact that α diversity is assessed based on sampling units whereas β diversity is calculated based on differences between sampling units (e.g., Legendre et al. 2005, Tuomisto and Ruokolainen 2006, Jost 2007). Accordingly, the number and quality of data points differ greatly. For example, in a study of 10 sites, 10 data points can be obtained for α diversity and 45 data points (pairwise similarity values) for β diversity. At the level of α diversity, species identities are irrelevant during data analysis, whereas at the level of β diversity it is the difference between the identities that is taken into account. At the level of α diversity, regression or correlation analyses as well as canonical analyses may be adequate (Magurran 2004). In contrast, at the level of β diversity, methods for comparing matrices have to be applied (e.g., the Mantel test) (Legendre and Legendre 1998). Thus, variances analyzed at these different levels of abstraction are not comparable and there is no simple relationship between them (Legendre et al. 2005), although numerous previous studies have confused them (Tuomisto and Ruokolainen 2006).

Within taxonomic groups, the conclusions drawn from patterns in α and β diversity can be similar (Clough et al. 2007), but may also differ greatly (Tylianakis et al. 2005) because two sites with equal species richness can share between all and none of their species. Local species richness of mobile taxonomic groups may approach regional species richness (Oliver et al. 1998), whereas assemblages of less mobile species are expected to differ between sites, leading to an increase in species turnover and, consequently, in regional diversity. Ultimately, the assumption that patterns for α and β diversity change in a similar way, which is underlying many biodiversity assessments, has been rarely tested and may not hold true (Tylianakis et al. 2005).

In the tropics, the congruence of diversity patterns between different taxa has mostly been studied across large geographical regions (e.g., Beccaloni and Gaston 1995, Carroll and Pearson 1998, Oliver et al. 1998, Myers et al. 2000, Moore et al. 2002, Duque et al. 2005, Tushabe et al. 2006, Larsen et al. 2007, McKnight et al. 2007). Only four studies have compared small-scale changes in taxonomically diverse groups along gradients of land use within tropical landscapes (Lawton et al. 1998, Schulze et al. 2004, Barlow et al. 2007, Nöske et al. 2008; see Plate 1). This paucity of studies is largely due to the difficulty of sampling and identifying the enormous biodiversity of tropical forests. As in most assessments of indicator taxa (Wolters et al. 2006), two of these studies focused only on the congruence of α diversity (Lawton et al. 1998, Schulze et al. 2004). Additionally, Barlow et al. (2007) and Nöske et al. (2008) also assessed congruencies between patterns of β diversity of various taxa along land-use gradients and found higher congruence of β diversity than of α diversity between taxa. However, their analyses were based on observed data for α diversity and a similarity matrix for β diversity and are therefore statistically incomparable. Furthermore, none of these studies compared α diversity with β diversity within taxa.

In the present study, we linked α and β diversity of four plant groups (trees, lianas, terrestrial herbs, epiphytic liverworts) and eight animal groups (birds, butterflies, lower canopy ants, lower canopy beetles, dung beetles, bees, wasps, and the parasitoids of the latter two) at 15 sites in natural rain forest and in three types of cacao agroforests differing in management in Sulawesi, Indonesia. For a direct comparison of α and β diversity, we analyzed α diversity not only with linear regressions, but also by comparing differences in species numbers, a level we called Δα (Appendix A), an additive analogue to the factorial similarity in species composition used in analyses of β diversity. Furthermore, because sampling is typically incomplete in species-rich tropical communities (Lawton et al. 1998), we compared observed species richness and similarity as well as estimated species richness and similarity indices (Colwell and Coddington 1994).
We focused our study on plants and insects as potential biological indicator taxa because they represent ~80% of all described species (Herrera and Pellmyr 2002) and determine important ecosystem processes (Loreau et al. 2001, 2003, Kremen 2005). In particular, because trees are the main structural elements of forests and represent crucial food resources for many vertebrates and insects (Daniels et al. 1992, Davis and Sutton 1998, Fermon et al. 2000, Greenberg et al. 2000, Willott et al. 2000, Green et al. 2005), they are commonly used to determine overall forest biodiversity (e.g., Oliver et al. 1998, Williams-Linera et al. 2005). Birds were included because they are the best-known major group of organisms and are much-used biodiversity indicators (Garson et al. 2002, Schulze et al. 2004, Jetz et al. 2007). By comparing the predictive values of $\alpha$, $\Delta\alpha$, and $\beta$ diversity of floral and faunal groups, we provide basis data for the use of indicator taxa in the design of policies that aim at biodiversity conservation in tropical landscapes.

**METHODS**

**Study area and site selection**

The study took place in an area of ~10 km$^2$ in and around the village of Toro in the Kulawi Valley, Central Sulawesi, Indonesia (1°30'24" S, 120°2'11" E, 800–900 m above sea level; Fig. 1). Toro is located at the western border of the 231 000-ha Lore Lindu National Park, ~100 km south of Palu, the capital city of Central Sulawesi. The region has an annual temperature of 24.0° ± 0.16°C (mean ± SE) and a monthly rainfall of 143.7 ± 22.74 mm. There are no clear seasonal precipitation fluctuations. The natural vegetation of the National Park around the village is submontane rain forest.

The agricultural landscape in the region is highly heterogeneous, consisting of a patchy mosaic of pasture, hedges, and cacao-dominated agroforests, which is typical for the region. Cacao production in the region increased strongly in the 1990s when large areas of coffee agroforest were converted into cacao agroforests (Steffan-Dewenter et al. 2007). Cacao agroforests in the...
Toro village are owned and managed by small-scale farmers. Shade tree management in the region is dynamic and farmers tend to remove shade trees in mature agroforestry systems to increase cacao production (Steffan-Dewenter et al. 2007). We defined a priori four habitat types with a gradient of shade tree diversity (Gradstein et al. 2007). (1) Mature forest sites (MF sites) were selected close to the village, but within the national park, at least 300 m away from forest sites where selective logging occurred, and representative of the submontane forest in the area (Kessler et al. 2005). In the selected sites minor rattan extraction occurred. (2) We chose cacao agroforests with diverse, natural shade trees (AN sites), retained after thinning of the previous forest cover and underplanted with cacao trees and few fruit trees. These sites had a long history of cultivation (approximately 20–40 years, converted from coffee to cacao agroforest approximately 10 years ago). These agroforests still had high numbers of native shade trees, including some endemic species. (3) We selected cacao agroforests with shade tree stands dominated by various species of planted shade trees (AD sites). These sites had a shorter history of cultivation between 15 and 20 years (cacao cultivation since approximately 10 years ago, sometimes converted from coffee agroforests), and the majority of the former forest canopy trees were replaced by various planted fruit and timber trees that provided the owners with non-market products. Among these trees were some native species, including a few endemics. (4) Cacao agroforests with a low diversity of planted shade trees (AF sites) had a history of cultivation after a clearcut 12–30 years ago (converted 4–12 years ago from coffee plantations, rice, or cornfields). Management of these agroforests was aimed at maximum cacao productivity. Shade was provided predominantly by the nonindigenous leguminous trees Gliricidia sepium (Jacq.) Walp. and Erythrina subumbrans Merr., which are nitrogen-fixing. Few native timber or fruit tree species were also grown, none of which were endemic.

We selected four replicates of each of the four habitat types, except for AN, where one plot had to be excluded from the analysis because the local owner cut many of the shade trees before our sampling was completed. Agroforest sites were selected based on the age of the cacao trees, which was at all sites between 4 and 17 years. At the time of this study, agroforestry was non-intensive in each site, with little use of fertilizers and pesticides. Farmers regularly pruned trees and weeded the plantations (two to four times per year).

The minimum distance between study sites was 300 m and the maximum distance was ~5 km. All sites were between 850 m and 1100 m above sea level. The agroforests did not have sharp borders with other habitat types, but gradually changed into other forms of land use and at the landscape scale formed a continuous band along the forest margin. Boundaries between agroforests were based on ownership rather than on any physical boundaries. We marked core areas of 50 × 50 m² in the middle of each site, whose land use and shade-tree composition was as constant as possible. Sites belonging to the different habitat types were geographically interspersed so that none of the individual habitat types were spatially clustered. Geographical distance between sites was calculated as the linear distance between the study plots based on GPS readings and was log-transformed prior to analysis.

Species collection and determination

Trees.—Each plot was subdivided into 25 subplots of 10 × 10 m². Within each subplot all trees with diameter at breast height (dbh; measured at 1.3 m above the ground surface) ≥10 cm were mapped and individually numbered with aluminum tags, their dbh was measured, and their trunk height and total height were estimated. Specimens of all recognizable morphospecies of trees were collected in sets of at least seven duplicates. Identification of the plant specimens was done by R. Pitopang, partly in collaboration with Dr. P. J. A. Kessler (Leiden, Holland), at Herbarium Celebense, CEB (Universitas Tadulako, Palu) and Herbarium Bogoriense, BO (Bogor). Vouchers were deposited in the herbaria BIOT, BO, CEB, GOET, and L. Specimens that could not reliably be named were grouped into morphospecies.

Lianas and herbs.—In each study plot of 50 × 50 m² 10 subplots of 2 × 2 m² each were randomly placed. Within these, all herb and liana species were inventoried, collected, and determined as detailed for the trees.

Epiphytic liverworts from lower canopy trees.—Two trees with a height up to 8 m, a dbh ranging between 20 and 60 cm, and comparable bark texture were selected in each study plot. In the agroforest sites these requirements for tree structure were fulfilled by cacao trees and in natural forest sites by trees in the understory. Each tree was divided into zone 1 (tree base up to the first ramification), zone 2 (inner crown), and zone 3 (outer crown), according to modified Johansson zones for small trees (Johansson 1974). Within subplots of 200 cm², liverworts were sampled from each cardinal direction in all three zones. The identification was carried out by M. Burghardt, S. R. Gradstein, and S. G. Sporn (Göttingen, Germany). Vouchers were deposited in CEB, GOET, and L. Specimens that could not reliably be named were sorted to morphospecies.

Birds.—In February and March 2007, each plot was visited on two mornings from 05:30 to 10:30. Birds were recorded visually and acoustically and by systematic tape recordings (Parker 1991, Abrahamczyk et al. 2008). For every species we recorded the number of individuals present simultaneously in the plot. During the second visit, only additional records (new species or more individuals of the same species) were considered. Species flying only above the canopy such as swifts (Apodidae) and raptors were excluded from the analysis. For taxonomy we followed Coates and Bishop (1997).
**Butterflies.**—Butterflies were captured alive in traps baited with rotten mashed bananas. A detailed description of the trap design can be found in Daily and Ehrlich (1995). Traps were suspended from tree branches with strings ~1.5 m above the ground. To prevent ants from entering the traps, branches touching the traps were removed and the string was prepared with sticky glue. At each location four traps were set up on the corners of each study plot. Trapping was conducted in March 2007, with nine days of trapping per study site. The majority of specimens could be identified in the field and, therefore, trapped specimens were released immediately afterwards. To avoid pseudoreplicates all butterflies were marked with a number on their forewing. Butterflies were identified according to Aoki et al. (1982), D’Abrera (1985), Tsukada et al. (1985), Tsukada (1991), and Vane-Wright and Fermon (2003). Butterfly communities are known to vary seasonally (Barlow et al. 2007), but in our study area seasonality appears to affect only the abundance of individual species and not species richness and composition (C. H. Schulze, unpublished data).

**Ants and beetles from lower canopy trees.**—Within each study plot, four trees were selected, which were of similar age and size. These were cacao trees in the agroforests (n = 48; height, 3.4 ± 0.56 m) and small, shade-dwelling lower canopy trees (n = 15; height, 6.3 ± 1.90 m) with canopy sizes similar to those of the selected cacao trees at natural forest sites. At one forest site, ants and beetles from only three trees could be sampled due to a technical problem. In order to characterize the forest insect fauna as completely as possible, we also sampled insects on a diverse set of trees in the forest understory. The 15 trees in the forest sites were identified by R. Pito Pang and belonged to 14 species of 10 families. Only on one occasion were two sampled trees in the same forest site of the same family. None of the forest trees were recorded flowering or fruiting at the time of sampling. At the time of the survey, cacao in the region was between a main flowering and a harvesting period, although minor flowering and fruiting occurred throughout the year. The lower canopy-dwelling ant and beetle fauna were sampled using canopy knockdown fogging, which is an effective and widely used technique for collecting arthropods from tree crowns (Perfecto et al. 1997, Lawton et al. 1998). With a SwingFog TF35, a fog of 1% pyrethroid insecticide (Permethrin; Mitra Envitech, Bogor, Indonesia) was blown horizontally into the target canopy to avoid collecting insects from higher canopy layers. Killed arthropods were collected from a 4-m² sheet of white canvas placed directly under each tree. We randomly selected one site per day and sampled all four trees between 08:00 and 09:00 at the time of day of lowest wind speed and rainfall probability between 17 December 2003 and 1 January 2004. The collected beetles and ants were sorted into units based on external morphology (morphospecies). Ant sorting was carried out by A. Rizali (IPB Bogor, Indonesia), based on literature (Bolton 1994) and reliable digital resources (available online).11 Beetles were identified and sorted by C. Bayer, B. Büche, and A. Rizali. Where necessary, beetle morphospecies were sorted based on genitalia preparations. All morphospecies were photographed and posted on the Internet through which more than 50 specialists internationally contributed with identifications based on the photographs and continued further taxonomic work.

**Dung beetles.**—Dung beetles were collected using baited pitfall traps as described in Shahabuddin et al. (2005). Traps were baited with ~20 g of fresh cattle (Bos taurus) dung. The dung was wrapped in a small square of textile and fixed with a string at the top of the trap, which was covered by a metal roof as protection against sun and rain. Five traps were set up along an 80-m transect and exposed for two days (Shahabuddin 2007). After removal from the traps, specimens were preserved in Scheerpelz solution (75% ethanol, 5% acetic acid, 20% water) as recommended by F. T. Krell (unpublished manuscript). Dung beetles were sampled once per month between March and August 2005. Identification of specimens was done in close collaboration with B. Büche (Berlin, Germany) using available keys (e.g., Baltsar 1963) and the reference collection of the Bogor Zoological Museum of LIPI (Bogor, Indonesia). Unidentified species were sorted to morphospecies.

**Bees, wasps, and their parasitoids.**—Trap nests offer standardized nesting sites for aboveground-nesting bees and wasps and can therefore be used to experimentally study these insects. They were constructed from PVC tubes with a length of 28 cm and a diameter of 14 cm. Internodes of the reed Saccharum spontaneum (Poaceae) with varying diameter (3–25 mm) and a length of 20 cm were inserted into these tubes to provide nesting sites (following Tscharntke et al. 1998). Twelve trap nests (four in each stratum) were installed from October 2004 until September 2005 in three different heights from understory (U) and intermediate tree height (I) to the canopy (C), where we placed the trap nests with a crossbow and a line. Trap nests were checked every month and bee and wasp larvae were reared for later identification. Understory was defined as below the cacao tree canopy, and trap nests were placed 1.5 m above ground. Intermediate height trap nests were placed above the cacao tree canopy and below the shade tree canopy (4 m above the ground in high-intensity plots and 7 m in primary forest, depending on canopy structure). Due to technical constraints we placed the canopy trap nests in the lower part of the shade tree canopy. Here, trap nest heights varied between forest habitat type due to different canopy heights, with higher nests in primary forests and low-intensity agroforestry systems (primary forest, 19.13 ± 0.438 m; low-intensity AF, 20.89 ± 0.746 m, n = 16,

11 (http://www.antweb.org) and (http://www.antbase.net)
respectively) and lower nests in medium- and high-intensity agroforestry systems (medium-intensity AF, 16.36 ± 0.619 m; high-intensity AF, 15.29 ± 0.844 m, n = 16, respectively). Sticky glue was applied every month to the edge of the PVC tube to deter ants from colonizing the trap nests. Individuals from the four trap nests per plot and stratum and the whole year were pooled for analysis.

Data analyses

α diversity.—For the analyses of αobs diversity we used the number of species recorded in each plot (Appendix A). Because observed species richness values in field studies are typically an underestimate of the actual number of species occurring at a site (Colwell and Coddington 1994), sampling completeness and estimated species richness (αest diversity) were also calculated using the Chao2 richness estimator (Chao 1987) with study sites as sample units, using the program EstimateS 8 Windows (Colwell 2006). The Chao2 estimator is recommended by Walther and Moore (2005) and is analogous to the estimator used for β diversity. To assess the potential impact of sampling completeness, we correlated sampling completeness with the correlation values.

Δα diversity.—In order to more directly compare α and β diversity, we calculated differences in species richness between plots using Mantel analyses. As for α diversity, this was done for the observed and the estimated richness values. The correlations of sampling completeness with the correlation values that involved two taxonomic groups were done using the lower of the two values of sampling completeness.

β diversity.—Similarities in the species composition of site pairs were quantified with the quantitative Sørensen similarity index (also known as Bray-Curtis index), which takes into account species abundances (Magurran 2004). To correct for incomplete sampling, we further used the similarity index of Chao et al. (2005), which is based on the above index but includes an estimation of incompleteness. As for α diversity, this was done for the observed and the estimated richness values, as well as correlating sampling completeness with the Mantel values.

Correlation analyses.—The correlation of diversity values between taxonomic groups was calculated using Spearman correlations (α diversity) and Mantel analyses (Δα and β diversity). Mantel analyses are correlation tests between matrices consisting of pairwise similarities or dissimilarities (Legendre and Legendre 1998). Probabilities are assigned by repeatedly randomizing the arrangement of similarity matrices, each time recalculating correlation coefficients and comparing the observed correlation value to the randomly generated ones. All Mantel analyses were conducted with PCOrd 4.5 (McCune and Mefford 1999), applying 9999 randomizations. Mantel analyses were also used to assess (1) the relationship between turnover in species composition (β diversity) and geographical distance between sites and (2) the relationship between Δα diversity and β diversity. Correspondences of the three measures of diversity (α, Δα, and β diversity) within study groups were assessed using Spearman correlations. When averaging R² values, two different approaches were used because many original R values had negative signs that were lost when squaring them. First, we did not consider negative values. Second, for those R² values based on negative R values, we maintained the signs. This was done because negative signs only can be considered to have high indication value (R² values) if the negative richness relationship between taxa is known a priori. Usually, however, the implicit assumption of biodiversity indication is that the diversity patterns of the taxa are positively correlated. In this case, R² values resulting from squaring negative R values would be misleading.

RESULTS

Species richness per site: α and Δα diversity

In total, we recorded 863 species, with total species richness per taxonomic group ranging from nine cavity-nesting bee species to 198 canopy beetle species (Table 1). Estimated sampling completeness ranged from 29% for canopy beetles to 89% for cavity-nesting bees (Table 1).

Patterns of species richness per sample site using the observed species numbers (αobs diversity) varied between taxonomic groups along the land-use gradient (Fig. 2). The αobs diversity of trees, lianas, liverworts, and dung beetles was highest in either mature forest stands or agroforest stands with natural shade trees and declined with decreasing shade-tree diversity, whereas that of herbs and canopy beetles showed the opposite pattern. With highest richness recorded in agroforests with diverse natural or planted shade trees, αobs diversity of butterflies, bees, wasps, and their parasitoids showed a hump-shaped pattern. Birds had an inversely hump-
shaped pattern, and ants were the only group with no clear response.

Linear correlation coefficients of $\alpha$ diversity per site between the different taxa varied enormously, ranging from $-0.92$ to $0.77$ (Figs. 2 and 3, Appendix B). Only 15 of the 66 pairwise comparisons were statistically significant and 10 of these significant correlations were negative. The same analysis based on richness values corrected for incomplete sampling with the Chao estimator for species richness ($\alpha$$_{est}$ diversity) resulted in similar overall results, with the correlation values of $\alpha$$_{obs}$ and $\alpha$$_{est}$ within study groups ranging from $R = 0.64$ for butterflies to 0.98 for parasitoids (mean for all groups, $R = 0.90$; Table 2).

A comparison of $\Delta\alpha$$_{obs}$ diversity among taxa using Mantel correlation analyses gave similar results to those obtained based on $\alpha$$_{obs}$ diversity (correlation between $\alpha$$_{obs}$ and $\Delta\alpha$, $R = 0.99$, $P < 0.001$), although $R$ values were lower and the number of significant relationships increased to 30 (15 negative; Fig. 3, Appendix B). Similar results were obtained comparing $\Delta\alpha$$_{est}$ and $\alpha$$_{est}$ diversity.

For none of the $\alpha$ diversity parameters were correlation coefficients between taxa significantly correlated with sampling completeness ($\alpha$$_{obs}$, $R = 0.09$, $P = 0.63$; $\alpha$$_{est}$, $R = 0.08$, $P = 0.69$; $\Delta\alpha$$_{obs}$, $R = 0.08$, $P = 0.69$; $\alpha$$_{est}$, $R = 0.03$, $P = 0.86$; $\Delta\alpha$$_{est}$, $R = 0.04$, $P = 0.76$), indicating that differential sampling completeness did not directionally bias the analyses.

Regional species richness: $\beta$ diversity

Mantel tests of correlations of $\beta$$_{obs}$ diversity between taxonomic groups recovered 37 significant relationships, all of which were positive (Fig. 3, Appendix B). Repeating the same analysis with values corrected for incomplete sampling ($\beta$$_{est}$ diversity) led to similar results (Table 2), although the correlation values were somewhat higher (Fig. 3, Appendix B). With the exception of liverworts, ants, and bees, which mostly showed low, nonsignificant correlation values of assemblage similarity with the other groups, turnover in the species composition of most study groups was significantly correlated.

Geographical distance between the study plots was significantly correlated with turnover in species composition only for birds, wasps, and parasitoids, in terms of $\beta$$_{obs}$ and $\beta$$_{est}$ diversity (Appendix B).

$\alpha$ and $\Delta\alpha$ vs. $\beta$ diversity

Within the study groups, patterns of $\alpha$ and $\Delta\alpha$ diversity were highly correlated, both for observed and
estimator-corrected values, with values ranging from $R = 0.62$ to $R = 1.00$ and averaging $R = 0.96$ (Table 2). Similarly, $\beta_{\text{obs}}$ and $\beta_{\text{est}}$ diversity were highly correlated ($R = 0.94$). In contrast, all comparisons of patterns of $\alpha$ and $\beta$ diversity resulted in low correlation values, ranging from $R = -0.35$ to $R = 0.56$ and averaging $R = 0.13$ (Table 2; Appendix B).

**DISCUSSION**

**$\alpha$ diversity**

Taxonomic groups differed greatly in their response to the change from natural forests to shaded cacao agroforests and the subsequent loss of shade-tree diversity. Species richness of trees, lianas, liverworts, and dung beetles declined with increasing land-use intensity, whereas species richness of the other taxa either did not respond at all (ants), had various hump-shaped responses (birds, butterflies, bees, wasps, and their parasitoids), or even increased (herbs and canopy beetles). This variability of $\alpha$ diversity patterns resulted in low congruence and predictability between the taxonomic groups (Figs. 1–3). The patterns of species richness were roughly similar when analyzed with the different measures ($\alpha_{\text{obs}}$, $\Delta\alpha_{\text{obs}}$, $\alpha_{\text{est}}$, and $\Delta\alpha_{\text{est}}$), which suggests that the method of analysis and sampling incompleteness did not strongly influence results (Fig. 3, Table 2).

One of the main questions of our study was the degree to which patterns of species richness of a given taxonomic group can be predicted by those of another. In our comparisons, only between 13% and 17% of the variance of species richness of one taxonomic group could be predicted by the species richness of another (Table 3). These values are in the range of those found by Lawton et al. (1998) for eight animal groups along a land-use gradient in Cameroon, but less than the 48% found by Schulze et al. (2004) for five groups in Indonesia and the 21–52% found by Barlow et al. (2007) for 15 groups in Brazil. These numerical differences likely reflect differences in the studied taxa as well as the extent of the land-use gradient. The
Table 2. Linear correlations (R values) between different diversity values within the 12 study groups.

<table>
<thead>
<tr>
<th>Group</th>
<th>( \gamma_{\text{obs}} - \gamma_{\text{est}} )</th>
<th>( \Delta \gamma_{\text{obs}} )</th>
<th>( \gamma_{\text{obs}} - \beta_{\text{obs}} )</th>
<th>( \Delta \gamma_{\text{obs}} )</th>
<th>( \beta_{\text{obs}} - \beta_{\text{est}} )</th>
<th>( \Delta \beta_{\text{obs}} )</th>
<th>( \gamma_{\text{est}} - \beta_{\text{est}} )</th>
<th>( \Delta \gamma_{\text{est}} )</th>
<th>( \beta_{\text{est}} - \beta_{\text{est}} )</th>
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<td>0.79</td>
<td>0.08</td>
<td>0.82</td>
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<td>0.11</td>
<td>0.11</td>
<td>0.79</td>
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<td>0.98</td>
<td>0.22</td>
<td>0.98</td>
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<td>0.34</td>
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<td>0.92</td>
<td>-0.11</td>
<td>0.18</td>
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<td>0.97</td>
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<td>0.95</td>
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<td>0.96</td>
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<tr>
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<td>0.99</td>
<td>0.90</td>
<td>0.11</td>
<td>0.17</td>
<td>0.90</td>
<td>0.99</td>
<td>0.07</td>
<td>0.16</td>
<td>0.90</td>
</tr>
</tbody>
</table>

Note: Abbreviations are: \( \gamma_{\text{obs}} \), observed alpha diversity, i.e., the counted species number per plot; \( \gamma_{\text{est}} \), estimated alpha diversity, i.e., the estimated total species number per plot; \( \Delta \gamma_{\text{obs}} \), the difference between the \( \gamma_{\text{obs}} \) values of two plots; \( \Delta \gamma_{\text{est}} \), the difference between the \( \gamma_{\text{est}} \) values of two plots; \( \beta_{\text{obs}} \), observed beta diversity, i.e., the observed similarity in species composition between two plots; \( \beta_{\text{est}} \), estimated beta diversity, i.e., the estimated similarity in species composition between two plots.

Habitats studied by Schulze et al. (2004) ranged from natural forests to annual crop fields devoid of trees, and those of Barlow et al. (2007) ranged from natural forests to Eucalyptus plantations. Our study focused on a comparatively limited range of natural forests and agroforestry systems. However, our R² values do not reflect the negative signs of many of the individual correlation (R) values. If these signs are maintained, then our average R² values range from −0.01 to 0.02 (Table 3). Thus, unless the nature of the diversity relationship between two given study groups was known a priori, the predictive value of patterns of species richness between study groups in our study was essentially zero. Thus, the differences between comparisons of taxonomic groups along tropical land-use gradients likely reflect differences in the study taxa as well as the extent of the land-use gradient.

The independent patterns that we recorded for the α diversity of a wide range of taxonomic groups are comparable with those reported by studies that compared taxa along natural ecotones. For example, along an elevational gradient in Costa Rica, richness of palms is highest at 100 m (Chazdon 1987), of trees at 300 m (Lieberman et al. 1996), of moths and vascular epiphytes at 1000 m (Cardelús et al. 2006, Brehm et al. 2007), and of ferns at 1800 m (Kluge et al. 2006). This difficulty of predicting patterns of species richness by indicator taxa has as well been documented for forests on different soil types in Amazonia (Duque et al. 2005, Tuomisto and Ruokolainen 2005) and for various taxa in Europe and North America (e.g., Prendergast 1997, Su et al. 2004, Wolters et al. 2006, Billetter et al. 2008).

Despite the fact that trees are the main structural elements of forests, tree species richness was in our study only positively correlated with the species richness of birds, dung beetles, and lianas. This result is in support of the idea that large groups of species depend on food resources that are not directly related to tree species richness, as has been suggested for canopy beetles (Wagner 2001), social bees (Klein et al. 2003), and canopy ants (Philpott and Foster 2005). For example, canopy beetle assemblages in the study area were dominated by species associated with dead wood and related fungi (M. M. Bos and B. Büche, unpublished data), while communities of canopy ants on cacao were mostly affected by microclimatic changes that were largely independent of changes in species richness of shade trees (Bos et al. 2007).

The observation of decreased species richness in five of seven studied insect groups in mature forest could be related to pronounced vertical stratification reported for tropical forest insects (e.g., Rodgers and Kitching 1998, DeVries et al. 1999, Schulze et al. 2001, Fermon et al. 2005, Diwakar and Balakrishnan 2007). While in some taxa species richness is more pronounced in one vegetation layer, others contribute equally to lower strata as well as the upper canopy (e.g., DeVries et al. 1997, Schulze et al. 2001, Stork and Grimbacher 2006). Natural and anthropogenic forest disturbance can cause a breakdown of vertical stratification as documented for butterflies in selectively logged forest (Dumbrell and Hill 2005, Fermon et al. 2005), at tree-fall gaps (Hill et al. 2001), and forest edges (DeVries et al. 1997). Consequently, lower vegetation strata at agroforestry sites, particularly sites at the forest edge, may be characterized by a rich mixture of canopy and understory species, while lower vegetation strata of forest interior sites are characterized predominantly by relatively few forest understory species.

### β diversity

Congruence of β diversity patterns between study groups was higher than between α diversity patterns (Figs. 2 and 3, Table 3). Unlike the results from the α diversity comparisons, the only negative correlations were found for liverworts. On average, 12–18% of the variance in β diversity could be predicted by that in another taxonomic group, although certain pairs of taxa
had much higher values, as exemplified by wasps and their parasitoids (76%) and wasps and canopy beetles (49%).

The low correlation coefficients between β diversity of bees and other study groups (even with their parasitoids) probably relate to the comparably even distribution of the nine aboveground nesting bee species in the study area, with most species present in all habitat types. In contrast, the other two “independent” study taxa, namely liverworts and ants, showed marked turnover between plots and habitats. Their low correlations to other study groups are presumably based on taxon-specific ecological requirements. Intriguingly, in Britain hot spots of liverwort diversity corresponded to cold spots of birds and butterflies (Prendergast et al. 1993). In the other taxonomic groups, variability in patterns of β diversity did not seem to relate to general taxonomic (e.g., plants vs. animals) or ecological (e.g., relative to trophic level, mobility) differences, but were rather group specific. For example, the extremely high turnover in beetle species relates to the fact that the majority of the recorded species aggregated on resources that were little related to habitat type, such as deadwood and fungi (M. M. Bos and B. Büche, unpublished data).

α vs. β diversity

In accordance with previous studies (e.g., Su et al. 2004, Tuomisto and Ruokolainen 2005, Barlow et al. 2007, McKnight et al. 2007, Nöske et al. 2008) our results show that among the 12 investigated groups, the use of indicator taxa is most valuable when taking into account the patterns in β diversity rather than α diversity. The higher congruence of patterns of β diversity than of α diversity is readily explained biologically (Su et al. 2004, McKnight et al. 2007, Rodrigues and Brooks 2007). Along an ecological gradient (land use, elevation, climate, soil fertility, etc.), β diversity of all taxa will tend to shift more strongly the more divergent the ecological conditions are. In contrast, species richness can be similar even under strikingly different conditions (Fig. 4).

Within the studied taxonomic groups, the congruence of patterns of α and β diversity was fairly low, with $R^2$ values averaging 0.07–0.20 (Table 3). Across the different taxa, only 1–4% of the variance of β diversity of a given group could be predicted by the patterns of α diversity of another group, and vice versa. If the sign of negative correlations is maintained in calculating these values, the values are further reduced to 0–1%. The main conclusion to be drawn from this is that indication of patterns of β diversity through patterns of α diversity of another taxon is practically impossible within our study system and difficult using the same taxon. These results are not surprising considering the low correlation values within each of the diversity levels and the fact

<table>
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<tr>
<th>Group</th>
<th>$\Delta\alpha_{obs}$</th>
<th>$\Delta\alpha_{est}$</th>
<th>$\Delta\beta_{obs}$</th>
<th>$\Delta\beta_{est}$</th>
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<tbody>
<tr>
<td></td>
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<td>$\beta_{est}$</td>
<td>$\alpha_{obs}$</td>
<td>$\alpha_{est}$</td>
</tr>
<tr>
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<td>–0.14</td>
<td>0.25</td>
<td>–0.07</td>
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<td>0.07</td>
<td>0.01</td>
<td>0.06</td>
<td>0.00</td>
</tr>
<tr>
<td>Herbs</td>
<td>0.29</td>
<td>–0.02</td>
<td>0.30</td>
<td>0.00</td>
</tr>
<tr>
<td>Liverworts</td>
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<td>–0.02</td>
<td>0.05</td>
<td>0.00</td>
</tr>
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<td>–0.09</td>
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<td>–0.05</td>
</tr>
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<td>0.00</td>
<td>0.05</td>
<td>0.03</td>
</tr>
<tr>
<td>Ants</td>
<td>0.07</td>
<td>0.04</td>
<td>0.09</td>
<td>0.05</td>
</tr>
<tr>
<td>Canopy beetles</td>
<td>0.15</td>
<td>0.04</td>
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<td>0.06</td>
</tr>
<tr>
<td>Dung beetles</td>
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<td>–0.02</td>
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</tr>
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<td>0.08</td>
</tr>
<tr>
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<td>–0.01</td>
<td>0.16</td>
<td>0.02</td>
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</table>

Notes: Because the directions of the relationships (negative, positive) are lost when $R^2$ values are squared, $R^2$ values were calculated both not maintaining the original signs (−) and maintaining them (+). Abbreviations are: $\alpha_{obs}$, observed alpha diversity, i.e., the counted species number per plot; $\alpha_{est}$, estimated alpha diversity, i.e., the estimated total species number per plot; $\Delta\alpha_{obs}$, the difference between the $\alpha_{obs}$ values of two plots; $\Delta\alpha_{est}$, the difference between the $\alpha_{est}$ values of two plots; $\beta_{obs}$, observed beta diversity, i.e., the observed similarity in species composition between two plots; $\beta_{est}$, estimated beta diversity, i.e., the estimated similarity in species composition between two plots.
that concordances across levels of diversity are necessarily less tight (Tylianakis et al. 2005, Clough et al. 2007).

Implications for biodiversity sampling

Our study shows that indication of diversity patterns of a given taxon by another taxon remains a difficult task (Prendergast 1997, Favreau et al. 2006, Wolters et al. 2006, Billeter et al. 2008). This has previously been shown for patterns of $\alpha$ diversity both at the local level (Lawton et al. 1998, Schulze et al. 2004, Favreau et al. 2006, Wolters et al. 2006) and on regional to continental scales (Beccaloni and Gaston 1995, Carroll and Pearson 1998, Myers et al. 2000, Moore et al. 2002, Tushabe et al. 2006, Billeter et al. 2008). We also found that different approaches to calculating $\alpha$ diversity (species numbers vs. differences between species numbers; observed vs. estimated values) resulted in roughly similar values. In particular, the sampling completeness of the different study groups did not appear to influence the observed patterns of $\alpha$ diversity directionally or in a predictable way.

Our study further showed that $\beta$ diversity is more consistent across the study taxa, and although overall levels of congruence were rather low (see also Tuomisto and Ruokolainen 2005, Nöske et al. 2008), negative correlation values were very rare and indication is possible, if on a low level. Furthermore, in contrast to $\alpha$ diversity, the correction for sampling incompleteness increased the indicative value of $\beta$ diversity, showing that this approach should be preferred when comparing $\beta$ diversity of incomplete samples.

Implications for biodiversity conservation in tropical landscapes

Because the potential conservation value of an area depends more on which species occur there, rather than how many species (Gaston 1996), the reasonably good
indication of $\beta$ diversity, in contrast to $\alpha$ diversity, is of considerable practical interest (McKnight et al. 2007). Due to contrasting patterns, indication of $\beta$ diversity through $\alpha$ diversity is also not possible, suggesting that diversity assessments based exclusively on patterns of $\alpha$ diversity miss the important $\beta$ diversity component. Perhaps most importantly, our study shows that, at least at the scale of our study, trees, despite being the main structural components of forests and agroforests and providing resources to many other organisms, are not better suited as indicators than other taxa. Whether the relatively high correlation values obtained for both $\alpha$ and $\beta$ diversity patterns for some taxon pairs such as trees and birds ($\alpha$ diversity) or wasps and their parasitoids ($\beta$ diversity) represent general relationships that can be used for biodiversity indication remains to be confirmed by further studies. Our results thus support those from other multi-taxon studies of the consequences of land-use change and suggest that the impact of management changes on the diversity and composition of a given taxon in tropical agroforests cannot be predicted reliably from other taxa, although changes in species composition ($\beta$ diversity) appear to be more consistent than those of species richness ($\alpha$ diversity).

ACKNOWLEDGMENTS

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LITERATURE CITED


APPENDIX A

An example of the calculation of the six different diversity parameters used in the study (Ecological Archives A019-090-A1).

APPENDIX B

Linear and Mantel correlations between study groups (Ecological Archives A019-090-A2).