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From forest to farmland: species richness patterns of trees and understorey plants along a gradient of forest conversion in Southwestern Cameroon

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Abstract. Vegetation surveys were carried out at 24 sampling stations distributed over four land use types, namely near-primary forest, secondary forest, agroforestry systems and annual crop lands in the northeastern part of the Korup region, Cameroon, to assess the impact of forest conversion on trees and understorey plants. Tree species richness decreased significantly with increasing level of habitat modification, being highest and almost equal in secondary and near-primary forests. Understorey plant species richness was significantly higher in annual crop lands than in other land use types. The four land use types differed in tree and understorey plant species composition, the difference being smaller among natural forests. Tree and understorey plant density differed significantly between habitat types. Density was strongly correlated with species richness, both for trees and understorey plants. Five tree and 15 understorey plant species showed significant responses to habitat. A 90% average drop in tree basal area from forest to farmland was registered. Our findings support the view that agroforestry systems with natural shade trees can serve to protect many forest species, but that especially annual crop lands could be redesigned to improve biodiversity conservation in agricultural landscapes of tropical rainforest regions.

Introduction

There is no doubt that primary rainforests are vanishing and that we are now living through the last decades of a vegetation dating back as far as 300 million years (Hallé 1990). The conversion of tropical primary forests into various land-use systems has serious impacts on distribution, community structure and population characteristics of flora and fauna (e.g. van Gemerden 2004; Waltert et al. 2005). In general, forest modification and clearance have negative impacts on biodiversity (e.g. Bawa and Seidler 1998) and, each 1% reduction of natural area will cost about 1% of steady-state diversity (Rosenzweig 2003). Thus, preserving small tracts of wild habitat can only delay these reductions (Rosenzweig 2003). To improve biodiversity conservation in tropical rainforest regions, it becomes crucial to redesign anthropogenic habitats so that their use is compatible with the use by a broad array of other species: this is a new strategy of conservation biology called "reconciliation ecology" that has grown out of a thorough understanding of species-area relationships (Rosenzweig 2003), see also (van Gemerden 2004). Rather than insist on protecting habitat from human use, reconciliation ecology works in and with the human dominated habitats that cover most of the terrestrial surface of the Earth (Rosenzweig 2003).

Various studies from all over the tropics deal with the question, how much biodiversity can be found in agricultural landscapes (e.g. Hughes et al. 2002; Schulze et al. 2004a; Waltert et al. 2004) but to date very few studies from tropical Africa exist (e.g. Devineau 1984; Malaisse 1984; Lawton et al. 1998; Zapfack et al. 2002; Waltert et al. 2005).

For Cameroon, Zapfack et al. (2002) found that the primary forest of the southern part of the country is the second plant species-rich habitat in the country, behind secondary forest, and the richest in non-timber forest products (e.g. medicinal plants, subsistence), when compared to land use types, while farmland is poorest, lacking large trees and harbouring just few useful ones. Given that cocoa plantations are potentially rich in medicinal as well as edible plants that can increase the peasant's revenues, Zapfack et al. (2002) recommended – in accordance with the reconciliation concept – that management strategies should include selection and reintroduction of original forest species into plantations of cocoa trees. Such management would also be beneficial for other taxa: there are strong correlations between tree diversity and diversity of birds and other forest-dependent biota (Waltert et al. 2005; Schulze et al. 2004a).

The objective of this paper is to assess the impacts of forest conversion on tree and understorey plant communities by comparing species richness and composition, as well as responses at individual species level, between natural forests (near-primary and secondary forest) and two land use types, agroforestry systems and annual crop lands. We also compared the density, diameter distribution and basal area of trees and, the density of understorey plants between the habitat types. Based on the results of Zapfack et al. (2002) we hypothesized that tree density and species richness would decrease with increasing habitat modification, but that abundance and species richness of understorey plants would peak in land use systems rather than forest. We also expected that species composition will change along the habitat gradient with forest species being gradually replaced by species of open country, and to find species-specific patterns of abundance along the habitat gradient.

Study area

The study was carried out in the Southwestern province of Cameroon, especially in the Northeastern part of the Korup Support Zone (KSZ) between the Eastern boundary of Korup National Park (KNP) and the Kwende Hills, precisely the area between Abat-Mgbegati-Basu-Bajo villages (see Figure 1). The area is part of the Guineo-Congolian forest, having a humid tropical climate where rainfall ranges from 1,500 to more than 10,000 mm per year, and giving rise to a variety of vegetation floristic regions (White 1983). The wettest period is from March to September, the remaining months are relatively dry. Temperatures range from 22 to 30 °C, with an average relative humidity of 87% throughout the year. The topography is generally undulating to rolling. Weathering is far advanced and leaching has been severe, and in spite of the high rainfall, little run-off occurs due to the free draining qualities of the soils. Under such conditions the soil formation process results in the formation of typical ferralitic soils. At low altitudes the parental material is of basalt origin which has flew from the Nkwende hills, leading to a soil dominated by clay, less stoney and suitable for farming systems, in which food crops, tree crops and forest trees are closely integrated (MINEF/KP 2002). Floristically, this area is part of the Hygrophylous Coastal Evergreen Rainforest that occurs along the Gulf of Biafra, and is part of the Cross-Sanaga-Bioko Coastal Forest ecoregion (Olsen et al. 2001, World Wildlife Fund 2001). This ecoregion is considered an important center of plant diversity because of its probable isolation during the Pleistocene (Davis et al. 1994) and holds an assemblage of endemic primates known as the Cameroon faunal group (see Oates 1996, Waltert et al. 2002). The region is also exceptionally rich in butterflies (Larsen 1997) and birds (e.g. Rodewald et al. 1994; Bobo et al. 2005).

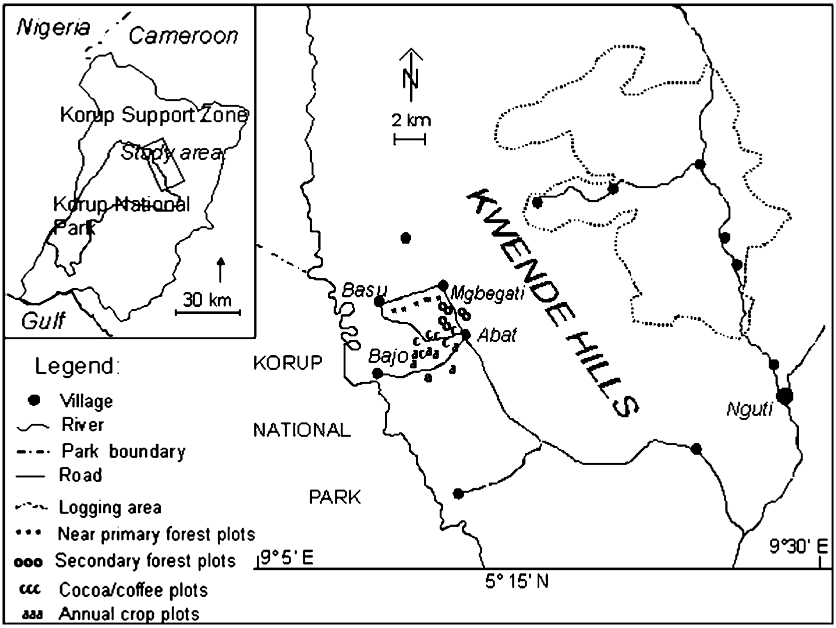

Figure 1. The study area.

The studied plots were all situated in the populated part of the KSZ, where farming is restricted to the immediate surroundings of the villages, leaving most of the area forested. The land use types chosen represent different forms of common land use practice, and are situated along a gradient of human disturbance where near-primary forest (NF) serves as a reference. They basically differ in two important characteristics of habitats (Horváth et al. 2001): Habitat complexity referring to the vertical structure of vegetation and habitat heterogeneity expressed in the horizontal variation of the habitat's features. All sites outside the near-primary forest, i.e. secondary forest (SF), agroforestry systems (CF) and annual crop farms (AC), are located at the vicinity of the forest edge. The main characterisitics of the chosen habitats are as follows (see also Waltert et al. 2005):

(1) NF: wet evergreen forest with high tree species richness. Closed canopy averages 35–45 m. The dominant trees are *Oubangia alata* and *Gilbertiodendron demonstrans*
(2) SF: moist evergreen forest which has been cleared for farming along roads about 15 years ago. These forests have a relatively closed canopy. Canopy height averages 25–30 m. The dominant trees are Oil palm *Elaeis guineensis* and, *Musanga cecropioides*
(3) CF: cocoa/coffee plantations shaded by natural forest trees of up to 25 m height. A part from Cocoa *Theobroma cacao* and Coffee *Coffea robusta* trees, Oil palm and Plum trees *Dacryodes edulis* are dominant
(4) AC: open monoculture of manioc, remnant forest trees, oil palms, no planted shade trees, dead wood, *Chromolaena odorata* and farmbush thickets; it is a dynamic habitat, due to the short cycles of the cultivated plants and associated human activities.

Methods

Data collection

For each of the four land use types defined above, six points were selected based on visual observations to guarantee certain homogeneity of plots for a same land use system (i.e. in total $4 \times 6 = 24$ sampling stations). Topographically, all these sampling stations were situated at an altitude of about 250 m above sea level (asl.). Study sites were plots of 50 m × 50 m, centred on the above-mentioned sampling stations. Each plot was divided into nine subplots of 10 m × 10 m (one subplot in the centre and eight others at the borders) so as to have 10 m in between subplots and covering 900 m^2 in total at each study site and where overstorey or tree species, number and diameter were recorded. In agroforestry sites, cocoa/coffee trees were not measured, but their numbers (based on 3 m × 3 m as space for a cocoa/coffee tree) and size classes were estimated for each plot. In each subplot, a 1 m × 1 m small plot established in their centre was used to collect data for understorey plants. Understorey plants are defined as all vascular plants of less than 1.3 m height, and the overstorey being all trees of more than 10 cm in diameter at 1.3 m height (DBH). In total, data were collected in 216 (9 subplots/smallplots ×24 sampling stations) point counts. All plants species were counted and identified at least to morphospecies level. Only the most common trees and understorey plants were identified to species level.

Data analysis

We counted for each study site, the total number of species of trees and understorey plants detected in the nine subplots/smallplots, here referred to as "observed" species richness. In most field studies, it is difficult to record all species present (see Nichols and Conroy 1996). Therefore, we also quantified an "estimated" species richness that takes into account the species which could not be recorded but which presence can be inferred from the pattern of observed species occurrence. To calculate estimated species richness, we used the first-order jackknife method that was initially designed to estimate population size from capture to recapture data, allowing capture probabilities to vary by individuals (Burnham and Overton 1978, 1979). This model can equally be applied to estimations of species richness (see Heltshe and Forrester 1983; Colwell and Coddington 1994; Boulinier et al. 1998; Chazdon et al. 1998; Nichols et al. 1998; Hughes et al. 2002). The Jackknife estimator is performing well if the proportion of rare species (those which are represented in only one or two samples) is low (Chao 1987; Nichols and Conroy 1996). We also calculated beta-diversity between different sites using the classic Soerensen (qualitative) index (Magurran 1988). To calculate first-order jackknife estimates at each site and beta-diversity between different sites, we used the computer program EstimateSWin7.0.0 of Colwell (2000) by randomizing samples 100 times. Parameters were used in a one-way ANOVA in order to analyse effects of land use type on species numbers. Means are given with standard deviation if not mentioned otherwise. Tukey's Honest Significance Difference-Test (HSD test) was used for multiple comparisons of means.

For each study site, abundance was expressed as the mean number of individuals detected at each study (900 m^2 for trees, 9 m^2 for understorey plants), and one-way ANOVA was done to detect species-specific responses to habitat variation. We applied the sequential Bonferroni technique (Holm 1979) to reduce the probability of statistical type I errors by calculating table-wide significances α for each species and listed only those species with $\alpha \leq 0.05$. Using *post-hoc* tests (Tukey's honest significant difference test), single species were assigned to different response categories.

We used the Morisita Horn index in a multidimensional scaling (StatSoft 2001) and ordinated our study sites two-dimensionally to depict similarity between habitat types. We also report the raw stress value φ, as well as its normative form (simply called "stress value") which is a measure of goodness-of-fit in non-linear multidimensional scaling, showing whether the original data are well-represented by the ordination (Cox & Cox 1994).

Spearman rank correlation coefficients r_s were also established to describe relationships between the tree density, basal area and understorey plant density, and tree and understorey plant species richness and abundance. Again, table-wide significances were calculated using the sequential Bonferroni correction (see Rice 1989). Spearman correlations, one-way ANOVA, and all other statistical analyses were performed using STATISTICA 6.0 (StatSoft 2001).

Results

Species richness of sampling station

Trees

In the 216 plots, a total of 856 tree records (single detections of tree individuals) belonging to 239 identified species were obtained. The number of tree records per sampling station was significantly affected by habitat type (One-way ANOVA, $F_{3,20} = 30.92$, $p < 0.001$). Tree numbers showed a clear decreasing pattern from NF to AC. Within the 50 m × 50 m plots of each sampling station, the number of accumulated records after the nine subplot surveys (replicates) was highest in near-primary forest (mean ± S.D.,308 ± 12.4), marginally lower in secondary forest (286 ± 50.9, Tukey's HSD test, $p = 0.87$), and significantly lower in agroforestry systems (204 ± 49.8, Tukey's HSD test, $p < 0.05$) and annual cultures (58 ± 12.4, Tukey's HSD test, $p < 0.001$).

Jackknife species richness estimators revealed that assemblages of the studied trees were not yet completely recorded: completeness of the inventories at single sites ranged from an average of 57.3% in the six annual crop land sites to 70.7% in the agroforestry sites. Observed species richness was significantly correlated with estimates ($r_s > 0.99$, $p < 0.001$, $N = 24$, see also Figure 2).

Highest species richness was found in the secondary forests with a mean number of 52.62 (±12.93) species; it was slightly lower in near-primary forest (50.69 ± 9.97) and was significantly lower in agroforestry systems (17.02 ± 7.4) and annual crop lands (11.07 ± 1.86) (One-way ANOVA, for estimated species: $F_{3,20} = 35.3$, $p < 0.001$) (see Figure 2).

Understorey plants

On the 216 plots, a total of 1230 understorey plant records (single detections of understorey plant individuals) belonging to 357 identified species were obtained. The number of understorey plant records per sampling station varied significantly among habitat type (One-way ANOVA, $F_{3,20} = 53.19$, $p < 0.001$). Within the 1 m × 1 m subplots of each sampling station, the number of accumulated records after the nine subplot surveys were highest in annual crop lands (529 ± 41.7) and significantly lower in secondary forests (364 ± 111.8, Tukey's HSD test, $p < 0.001$), near-primary forests (200 ± 26.3, Tukey's HSD test, $p < 0.001$) and agroforestry systems CF (137 ± 21.2 Tukey's HSD test, $p < 0.001$).

Jackknife species richness estimators revealed that assemblages of the studied understorey plants were not yet completely recorded: completeness of the inventories at single sites ranged from an average of 57.1% in the six NF sites to 64% in the six AC sites. Observed numbers of recorded species were significantly correlated with estimates ($r_s > 0.99$, $p < 0.001$; $N = 24$, see also Figure 3).

The high number of accumulated records in annual crop lands was also reflected by the highest number of estimated species richness in this land use type with a mean number of 76.69 (±16.8), which was significantly lower in secondary forest (59.24 ± 7.19), near-primary forest (36.85 ± 7.67) and agroforestry systems (22.98 ± 3.73) (One-way ANOVA, for estimated species: $F_{3,20} = 44.6$, $p < 0.001$) (see Figure 3).

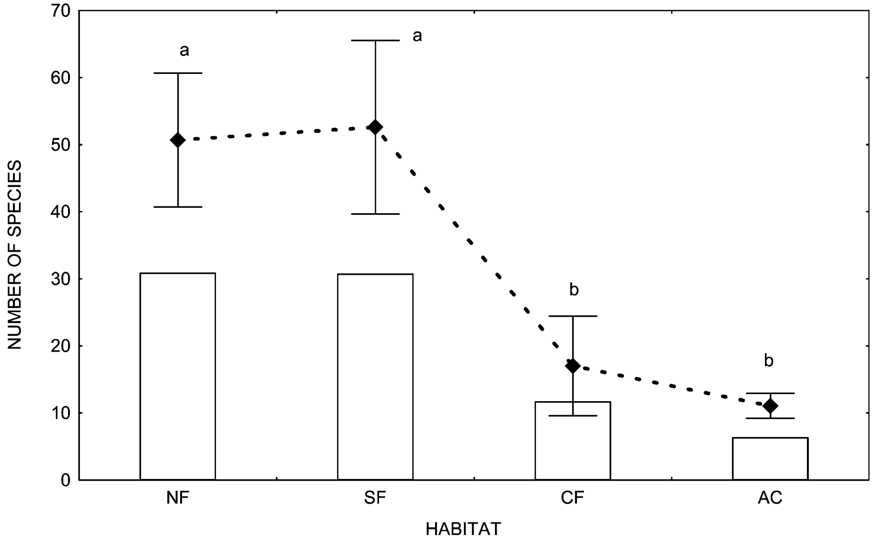

Figure 2. Mean species richness (±S.D.) given as estimated number of tree species (dotted line) based on the first-order jackknife method. Additionally, the observed species richness (bars) is presented. Different letters indicate significant differences (Tukey's Honest Significant Difference-Test) between mean estimated species richness.

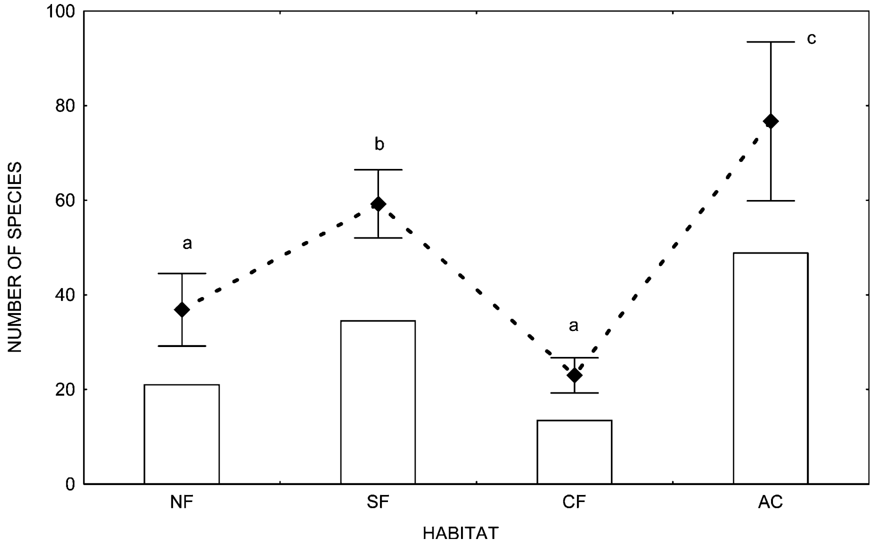

Figure 3. Mean species richness (±S.D.) given as estimated number of understorey plant species (dotted line) based on the first-order jackknife method. Additionally, the observed species richness (bars) is presented. Different letters indicate significant differences (Tukey's Honest Significant Difference-Test) between mean estimated species richness.

Species similarities, abundance and composition

Trees

Pairwise similarity of tree species composition (mean Soerensen incidence index ± S.D.) was highest among the six agroforestry sites (0.34 ± 074). It was lower in the six secondary forest sites (0.21 ± 0.06) and very low among the six near-primary forest sites (0.17 ± 0.081) and the six annual crop land sites (0.17 ± 0.11). It was very low between agroforestry systems and annual cultures (0.16 ± 0.13), agroforestry systems and secondary forest (0.13 ± 0.073), near-primary and secondary forest sites (0.10 ± 0.075), and almost null between near-primary forest and agroforestry sites (0.045 ± 0.045), secondary forest and annual crop land sites (0.08 ± 0.06), and near-primary forest and annual crop land sites (0.03 ± 0.045).

Two-dimensional ordination of study sites using abundance data in a multidimensional scaling showed overlap between habitats, particularly between near-primary and secondary forest, and between secondary forest and annual crop land sites, confirming that there are still some natural trees left in crop farms. Agroforestry systems did not show an overlap between any of the other habitat types. This can be explained by the fact that natural trees are removed for the production of cocoa/coffee that need more light at certain age of their development (Figure 4). A one-way MANOVA of the sample scores extracted from the two-dimensional ordination revealed a significant difference between the four groups of sites (Rao's $R_{6,38}$ = 13.36, $p < 0.001$). Two-dimensional ordination was deemed sufficient due to its low stress value (raw stress value φ = 19.72; stress value = 0.185).

The most often recorded trees in NF were regenerating trees and shrubs characteristic of mature rainforest known as *Oubanguia alata*, *Gilbertiodendron demonstrans*. SF were dominated by gap and fast growing species such as *Pycnanthus*, *Rauvolfia*, or *Musanga spp.*, with scattered oil palms *Elaeis guineensis* distribution. Apart from cocoa/coffee trees, the most common tree species on CF and AC lands were oil palms *Elaeis guineensis*, plum *Dacryodes edulis* and *Ricinodendron heudelotii* trees.

Understorey plants

Pairwise similarity of understorey plant species composition (mean Soerensen incidence index ± S.D.) was highest among the six annual culture sites (0.33 ± 0.07), slightly lower among the six agroforestry sites (0.27 ± 0.08) and the six secondary forest sites (0.23 ± 0.05) and very low among the six near-primary forest sites (0.15 ± 0.07). It was almost null between any of the following habitats: between agroforestry and secondary forest (0.08 ± 0.05), near-primary and secondary forest (0.07 ± 0.05), agroforestry systems and annual crop lands (0.04 ± 0.03), secondary forest and annual crop lands (0.04 ± 0.03), near-primary forest and agroforestry systems (0.02 ± 0.03), and near-primary forest and annual cultures (0.01 ± 0.02).

Multidimensional scaling revealed no considerable overlap in species composition between habitats, again confirming that species compositions were very different from one habitat type to another. Nevertheless, near-primary forest sites seemed to be closer to secondary forest sites as compared to other

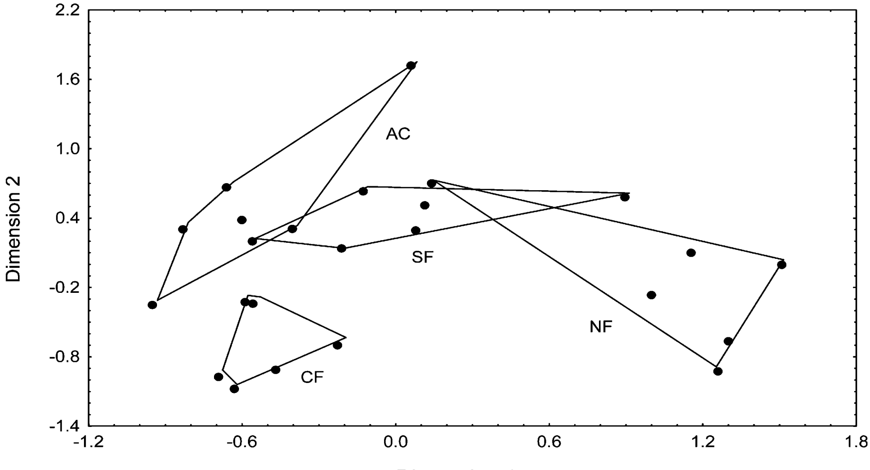

Figure 4. Multidimensional scaling of tree species composition at different sampling stations based on abundance data. Sampling stations belonging to the same habitat category are connected by lines.

habitat types (Figure 5). A one-way MANOVA of the sample scores extracted from the two-dimensional ordination revealed a significant difference between the four groups of sites (Rao's $R_{6,38} = 35.15, p < 0.001$). Also for this dataset, two-dimensional ordination was found being sufficient (raw stress value $\varphi = 14.68$; stress value = 0.160).

In near-primary forest sites, mainly rainforest shrubs such as *Scaphopetalum, Cola* spp. (Sterculiaceae), or *Gilbertiodendron demonstrans* (Caesalpiniaceae) dominated the understorey vegetation. Small shrubs such as *Rinorea subintegrifolia* (Violaceae) and monocotyledons such as *Anubias* spp., *Raphidophora africana* (and other Araceae), *Afromomum* spp. (Zingiberaceae) were common in SF. Herbs equally dominated the understorey of CF sites, with Araceae (*Anchomanes difformis*), Maranthaceae (*Maranthochloa* sp.) or Acanthaceae (*Brillantaisia* sp.) as representatives. Understory plant species of AC were mainly those subject to cultivations, such as cassava (*Manihot* spp.), Maize (*Zea mays*), Groundnut (*Arachis hypogaea*), beans (*Phaseolus* spp.), taro and cocoyam (*Colocasia* spp.), but also the invasive pioneer *Chromolaena odorata* (Asteraceae) was frequently recorded.

Species level responses to habitat types

Trees

Out of the 239 tree species recorded in the 24 sampling stations, 20 species showed significant responses to habitat type (ANOVAs, $p \leq 0.05$). When

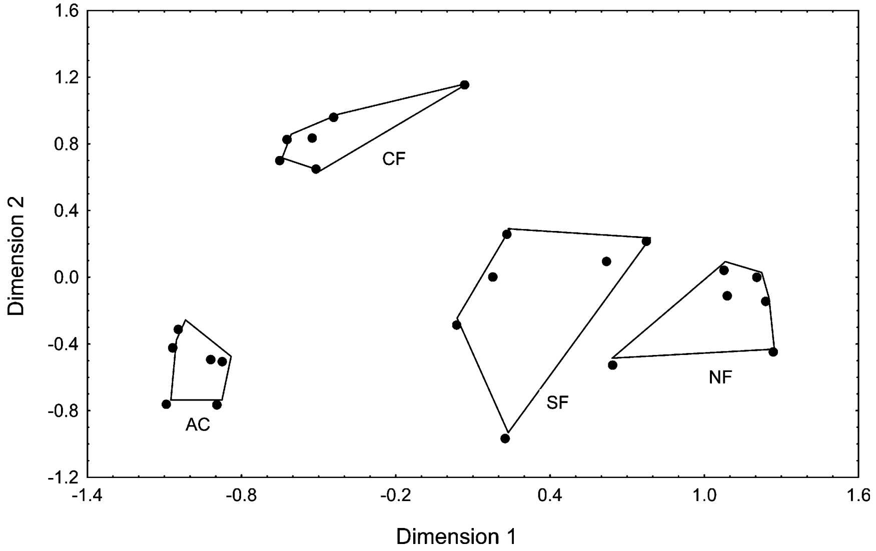

Figure 5. Multidimensional scaling of understorey plant species composition at different sampling stations based on abundance data. Sampling stations belonging to the same habitat category are connected by lines.

applying sequential Bonferroni correction to this list of species, responses to habitat type are significant only in five species (Table 1). Based on ANOVA and *post-hoc* tests (Tukey's HSD test, $p < 0.05$), three main categories of responses were defined. In response category 1, only one species, *Annickia chlorantha* was significantly more abundant in both natural forests as compared to land use systems. In response category 2, two species *Albizia ferruginea* and *Petitocodon parviflora* were significantly more abundant in secondary forest sites as compared to other habitats. In response category 3, the two planted species *Coffea robusta* and *Theobroma cacao* were found almost exclusively in agroforestry sites (Table 1). It should be noted that there were 148 tree species (i.e. 62% of recorded species) that are present in only one of the 24 plots established for this study.

Understorey plants

Out of the 357 recorded understorey plant species in the 24 sampling stations, 46 showed significant responses to habitat type (ANOVAs, $p \leq 0.05$). When applying sequential Bonferroni correction to this list of species, responses to habitat type are still significant in 15 species (Table 2). Based on ANOVA and *post-hoc* tests (Tukey's HSD test, $p < 0.05$), three main categories of responses were defined. In response category 1, only one species, the *Scaphopetalum blaekii*, was significantly abundant in both natural habitats, with a total absence in agroforestry and annual crop lands. In response category 2, three species, *Leptoderris ledermannii, Rinorea subintegrifolia* and *Afromomum* sp., were significantly more abundant in secondary forest sites as compared to near-primary forest sites and completely absent from agroforestry systems and annual crop lands. In response category 3, 11 species were just present in

Table 1. Tree species with significant responses to habitat type, after sequential Bonferroni correction.

Species	n	Habitat Near primary forest	Secondary forest	Agroforestry systems	Annual crops	$F_{3,20}$	$\alpha \leq$	Cat.	Highest abundance
Coffea robusta	56	0.0 (0.0)	0.2 (0.4)	7.5 (0.4)	0.2 (0.4)	13.67	0.001	3	CF
Theobroma cacao	56	0.0 (0.0)	0.2 (0.4)	7.5 (0.4)	0.2 (0.4)	13.67	0.001	3	CF
Albizia ferruginea	7	0.0 (0.0)	0.8 (0.4)	0.3 (0.4)	0.0 (0.0)	11.33	0.01	2	SF
Petitocodon parviflora	4	0.0 (0.0)	0.7 (0.5)	0.0 (0.0)	0.0 (0.0)	10.00	0.05	2	SF
Annickia chlorantha	5	0.7 (0.5)	0.2 (0.4)	0.0 (0.0)	0.0 (0.0)	5.51	0.05	1	NF, SF

Tree abundance expressed as total number of individuals recorded (n), and given for each habitat type as mean (± S.D.) number of individuals recorded at each study site (900 m^2). Results of one-way ANOVA, table wide significance (α), as well as response category and preferred habitat type are also given.

Table 2. Understorey plant species with significant responses to habitat type, after sequential Bonferroni correction.

Species	*n*	Habitat Near primary forest	Secondary forest	Agroforestry systems	Annual crops	$F_{3,20}$	$\alpha\leq$	Cat.	Highest abundance
Leptoderris ledermannii	10	0.2 (0.4)	1.5 (0.5)	0.0 (0.0)	0.0 (0.0)	27.14	0.001	2	SF
Blighia sp.	10	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.8 (0.4)	25.00	0.001	3	AC
Costus lucianusianus	10	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.8 (0.4)	25.00	0.001	3	AC
Cyathula sp.	6	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.7 (0.5)	25.00	0.001	3	AC
Sporobolus sp.	6	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.8 (0.4)	25.00	0.001	3	AC
Triumpheta cordifolia	6	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.8 (0.4)	25.00	0.001	3	AC
Rinorea subintegrifolia	21	0.5 (0.8)	1.5 (0.5)	0.0 (0.0)	0.0 (0.0)	12.00	0.01	2	SF
Afromomum sp.	15	0.0 (0.0)	1.3 (1.0)	0.0 (0.0)	0.0 (0.0)	10.00	0.05	2	SF
Aspilia africana	9	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.7 (0.5)	10.00	0.05	3	AC
Discorea sp.	7	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.7 (0.5)	10.00	0.05	3	AC
Lusticia insularis	16	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.7 (0.5)	10.00	0.05	3	AC
Manihot utilissima	19	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.7 (0.5)	10.00	0.05	3	AC
Verbenaceae sp.1	5	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.7 (0.5)	10.00	0.05	3	AC
Albizia zygia	11	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.7 (0.5)	10.00	0.05	3	AC
Scaphopetalum blaekii	50	2.3 (1.5)	1.2 (1.0)	0.0 (0.0)	0.0 (0.0)	9.26	0.05	1	NF, SF

Understorey plants abundance expressed as total number of individuals recorded (*n*), and given for each habitat type as mean (±S.D.) number of individuals recorded at each study site (9 m^2). Number of individuals recorded (*n*), results of one-way ANOVA, table wide significance (α), as well as response category and preferred habitat type are also given.

annual crop land sites (Table 2). There were also 138 understorey plant species (i.e. 39% of recorded species) present only in one of the 24 plots established for this study.

Vegetation structure and basal area

Some vegetation parameters of the study sites have been already described in Bobo et al. (2004) and Waltert et al. (2005). Here, only some important results are included for completeness (see Tables 3 and 4). Both tree density (the number of trees per 900 m^2) and basal area were significantly different between habitat types, showing a clear decrease from forest to farmland habitat (Table 3), with highest tree density (cocoa/coffee trees excluded) recorded on near-primary forest sites followed by secondary forest sites between which no significant differences were found (Tukey's HSD test, $p = 0.87$ for numbers of trees, $p = 0.65$ for basal area). Tree density (excluding cocoa/coffee) was significantly lower in agroforestry systems than in both natural forests (Tukey's HSD test, $p < 0.05$) with a reduction of 33.7% compared to near-primary forest sites, whereas basal area was not (Tukey's HSD test, $p > 0.17$). This shows that the studied agroforestry sites still possess a good stock of remnant forest trees, with *ca.* 70% of the tree density and basal area of the studied near-primary forest. Annual crop lands had the lowest trees density and basal area, representing *ca.* 20% and 10% of what was found in near-primary forest, respectively. Understory plant density also differed significantly between habitats (Table 3). Nearly twice as much understory plants were found in secondary forests and nearly three times as much in agroforestry systems than near-primary forests (Tukey's HSD test, all $p < 0.001$). Understory plant density was only marginally lower in agroforestry systems than in near-primary forests (Tukey's HSD test, $p = 0.28$).

In order to describe the diameter distributions of trees, we pooled data from different study sites per habitat (Table 4): Secondary forests differed from near-primary forests in a lowered frequency of trees of the 21–30 cm dbh size class, as well as in some larger size classes (61–80 cm dbh, and 91–100 cm dbh), but was otherwise similar to that of the near-primary forests. Both vegetation types seemed to have a high regeneration capacity with the highest number of trees in the lowest diameter class (10–20 cm dbh). The main difference between agroforestry systems and annual crop lands was the absence of large trees above 80 cm dbh in annual cultivations. The distribution of trees into diameter categories tends to be more even in near-primary forest and secondary forest sites. Agroforestry sites (when taken into account the planted cash crop trees) and annual crop land sites sites exhibited a rather irregular tree distribution into diameter classes.

Table 3. Mean density of trees and understorey plants and mean tree basal area (±S.D.) per habitat type.

	Habitat type				$F_{3,20}$	$p<$
	Near-primary forest	Secondary Forest	Agroforestry Systems	Annual cultures		
Tree density [Ind./900 m^2]	51.3 (±12.0)	47.7 (±8.1)	34.0 (±7.9)	9.7 (±2.0)	30.92	0.001
Tree basal area [m^2/ha]	48.7 (±14.6)	40.0 (±19.7)	32.7 (±7.1)	4.9 (±3.9)	12.85	0.001
Understorey plant density [Ind./9 m^2]	33.3 (±4.2)	60.7 (±17.8)	22.8 (±3.4)	88.2 (±6.6)	53.19	0.001

Planted cocoa/coffee trees are excluded from the agroforestry data (see also Bobo et al. 2004, Waltert et al. 2005).

Table 4. Diameter distribution of tree species within the land use systems.

Diameter class (cm)	Near-primary forest		Secondary forest		Cocoa/coffee plantation		Annual crops	
	No.	%	No.	%	No.	%	No.	%
10–20	172	55.84	164	57.34	25	12.25	18	31.03
21–30	69	22.4	41	14.3	15 (480)	7.35	4	6.9
31–40	23	7.47	26	9.09	13 (120)	6.37	6	10.3
41–50	9	2.92	9	3.15	11	5.39	1	1.72
51–60	13	4.22	14	4.9	6	2.94	4	6.9
61–70	6	1.95	0	0	2	0.98	0	0
71–80	2	0.65	0	0	1	0.49	1	1.72
81–90	1	0.32	3	1.05	3	1.47	0	0
91–100	6	1.95	0	0	0	0	0	0
101–110	1	0.32	3	1.05	5	2.45	0	0
>110	2	0.65	3	1.05	3	1.47	0	0

Numbers of trees and percentage per 5400 m^2 (900 m^2/plot × 6 plots per habitat) are given. In brackets, are the estimated figures for cocoa/coffee trees. (see also Waltert et al. 2005).

Correlations between vegetation parameters (density and basal area) and species richness and abundance

Out of the 10 Spearman rank correlations between vegetation parameters (density, basal area, and species richness) listed in Table 5, seven were significant on the 5% level (Table 5). Density and species richness was very strongly correlated both for trees and for understorey plants. Understorey plant species richness and density were moderately negatively correlated with tree density. Strongly negative correlations were found between tree basal area and understorey plant species richness and density. Trees basal area and tree density were moderately positively correlated. There were no significant correlations between tree basal area and tree species richness, nor between understorey plant density and tree species richness, and between tree species richness and understorey plant species richness (Table 5).

Table 5. Spearman rank correlation coefficients r_s of correlations between species richness, density and basal area of trees and/or understorey plants ($n = 24$ study sites in all cases).

	Tree species richness	Tree density	Tree basal area	Understorey plant species richness
Tree species richness	/			
Tree density	0.87***			
Tree basal area	n.s.	0.57*		
Understorey plant species richness	n.s.	−0.44*	−0.74***	
Understorey plant density	n.s.	−0.58*	−0.76***	0.92***

Bonferroni corrected table-wide significance level * $\alpha < 0.05$, *** <0.001.

Discussion

Our study showed that species richness of trees and understorey plants were affected by forest modification and land use systems. Both groups of plants changed strongly in their composition during the transition from forest to farmland (also in White 1992; Sokpon 1995; Sonké 1998; Sonké and Lejoly 1998; Zapfack et al. 2002; Schulze et al. 2004a, 2004b), giving space for the development of fast growing and invasive weed species like *Chromolaena odorata* (Asteraceae).

Annual crop land sites had the lowest tree species richness and the highest understorey plant species richness. This can be explained by the way people manage farms in Cameroon, leaving weeds growing among crops and small fallowlands bordering cultivated areas. In other geographical regions, agricultural areas are probably more regularly cleaned leaving the ground barred (Schulze et al. 2004a, b). In such areas, annual cultivations have a much lower plant diversity of the herb layer (understorey plants) as compared to natural forests.

In our study area, the reduction of tree species richness from forest to farmland was found to be 79.5%. Along the habitat gradient, an increase of 57% in understorey plant species richness was also recorded (annual crop compared to near-primary forest sites). The reported tree species loss is considered very high when compared to the 19% found by Turner et al. (1994) in Singapore as a result of logging activities and land conversions.

In agroforestry sites, the reduction in tree species richness was still high *ca*. 62.1% as compared to near-primary forest. Agroforestry sites had the lowest understorey plant species richness, as was also observed elsewhere (Schulze et al. 2004a, b), and were 72.4% poorer than annual crop land sites because of the shade by cocoa/coffee trees that inhibited light to reach the ground. Also, the low rate of cocoa/coffee leaves decomposition resulting in an accumulation of dry matter on the soil, and surely also the period of the year (Zapfack et al. 2002), could explain this low understorey plant species richness in agroforestry systems.

Secondary and primary forest sites had highest, and nearly equal, tree species richness. Zapfack et al. (2002) also found similarly high tree species richness in secondary and primary forests, but found a dominance of pioneer species in the secondary vegetation that has enhanced the recovery process after disturbance (see also van Gemerden 2004). Understorey plant species richness was higher in secondary than in near-primary forest sites because of higher light level at the ground of secondary vegetation that favours many light-demanding herbaceous species.

The low Soerensen incidences of tree and understorey plant species between the four groups of sites showed the low level of similarity between the studied plant communities, indicating a high species turnover. This is similar to Zapfack's et al. (2002) findings. The low Soerensen indices of trees (17%) obtained among our near-primary forest sites is in the same range as reported elsewhere in the tropics (i.e. between 7.8 and 15.7%, Zent and Zent 2004). A relatively high proportion of singleton species per plot (55.4% of all tree species in our near-primary sites) as well as the high proportion of the entire species inventory of species that are unique to a single plot (62% of recorded tree species in our studied sites) can partially explain this low intersite similarity.

Tree basal area in our study clearly decreased from near-primary to annual crop land sites. But, in Ivory Coast, Democratic Republic of Congo and Southern Cameroon, Devineau (1984), Malaise (1984) and Zapfack et al. (2002) found different patterns, showing a peak in secondary forest (44.9 m^2/ha) and almost a null value (0.07 m^2/ha) in annual crop lands. The basal area of 48.7 m^2/ha from our near-primary forest sites, was higher than what was found in Southern Cameroon (i.e. 39.2 m^2/ha, Zapfack et al. 2002), where no tree with diameter at breast height higher than 110 cm was recorded, indicating former logging activities. It was also higher than the values (29.7–42.6 m^2/ha) obtained elsewhere in the South province of Cameroon where some large trees (e.g. dbh = 143 cm) can still be found despite ancient selective logging activities (van Gemerden 2004). In the Lomako–Yekokora interfluvium forest of the Democratic Republic of Congo, basal areas range from 29.0 to 43.8 m^2/ha (Boubli et al. 2004). In the four forest plots of Sierra Maigualida in Venezuelan Guayana, values between 20.56 and 40.83 m^2/ha were obtained for the basal area (Zent and Zent 2004). We found indication of a good stock of remnant forest trees e.g. *Funtumia elastica*, *Rauvolfia vomitoria*, moabi *Baillonella toxisperma*, bush mango *Irvingia* spp., completed by some multi-purpose planted trees like e.g. oil palms *Elaeis guineensis*, plum *Dacryodes edulis*, are left in agroforestry site (see also Zapfack 2002). Our annual crop sites still possessed numbers of medium sized trees comparable to annual cultivations in Ivory Coast (Devineau 1984), Democratic Republic of Congo (Malaisse 1984) and South Cameroon (Zapfack et al. 2002), corresponding to a reduction of *ca*. 90% of the original basal area.

A classic tree distribution into diameter classes, i.e skewed towards the smaller classes, were found in near-primary and secondary forests (see also van Gemerden 2004, Boubli et al. 2004), while agroforestry systems (when taken into account the planted cash crop trees) and annual crop lands exhibited an irregular tree distribution, more likely a sign of higher disturbance level. The same findings were made in other tropical rainforests (Zapfack et al. 2002, Malaisse 1984, Devineau 1984).

Along the gradient of disturbance in our study area, the densities and species richness of trees were negatively affected. In general, the higher the density the higher the species richness, resulting in a high correlation between these two factors (Zapfack's et al. 2002). Tree basal area seemed to have a strong negative influence on the density and species richness of understorey plants, explaining why the soil level of primary forest is almost barred.

Conclusion

This study showed that tree basal area, tree density, tree diameter distribution, and species composition is greatly reduced in tropical land use systems and that restoration of original forest trees could be used to achieve conservation objectives when redesigning land use systems in tropical rainforest regions. Basal area of natural trees could be much higher particularly in cocoa/coffee plantations as these cash crops have lost their economic importance in tropical rural areas due to severe drop of prices on the world market. Such an improvement could also be assisted by reintroducing forest tree species that are known to have multi-functions in the daily live of local people. Replanting wild edible fruits and removing some cocoa/coffee trees will help the peasants to increase their income. Replanting medicinal plants in cocoa/coffee farms will reduce local people expenses on medicine, as well as time by preventing them to go far in the forest to fetch medicinal plants. In agroforestry systems of our study area, existing tree densities (*ca.* 380 trees/ha) are already considerable, but some cocoa/coffee trees still need to be removed to improve the light condition on the ground and to favour other plant species and some related taxa (e.g. butterflies, Schulze et al. 2004b). This will in the long run improve the species richness and composition of this anthropogenic habitat. The growth of tree species to a bigger diameter (>80 cm dbh) in annual crop lands should be favoured by advising the peasants not to kill or cut prominent useful shrubs in their farms or fallow lands. Some useful trees can even be planted where the land is bared to protect and improve the soil conditions. All these actions should be done gradually in time and space to achieve near-natural diameter distribution and tree species composition, and to avoid any further alteration of ecological functions of land use systems in tropical rainforest regions.

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