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Floristic diversity in fragmented Afromontane rainforests: Altitudinal variation and conservation importance

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Abstract

Question: How does the floristic diversity of Afromontane rainforests change along an altitudinal gradient? What are the implications for conservation planning in these strongly fragmented forest areas that form part of the Eastern Afromontane Biodiversity Hotspot?

Location: Bonga, southwestern Ethiopia.

Methods: Based on evidence from other montane forests, we hypothesized that altitude has an effect on the floristic diversity of Afromontane rainforests in southwestern Ethiopia. To test this hypothesis, detailed vegetation surveys were carried out in 62 study plots located in four relatively undisturbed forest fragments situated at altitudes between 1600 m and 2300 m. Floristic diversity was evaluated using a combination of multivariate statistical analyses and diversity indices.

Results: Ordination and indicator species analyses showed gradual variations in floristic diversity along the altitudinal gradient with a pronounced shift in species composition at ca. 1830 m. Upper montane forest (> 1830 m) is characterized by high fern diversity and indicator species that are Afromontane endemics. Lower montane forest (< 1830 m) exhibits a greater diversity of tree species and a higher abundance of the flagship species *Coffea arabica*.

Conclusions: Our results provide crucial ecological background information concerning the montane rainforests of Ethiopia, which have been poorly studied until now. We conclude that both forest types identified during this study need to be considered for conservation because of their particular species compositions. Owing to the high degree of forest fragmentation, conservation concepts should consider a multi-site approach with at least two protected areas at different altitudinal levels.

Keywords: *Coffea arabica*; East Africa; Ordination; Plant diversity; Protected area; Tropical montane forest.

Nomenclature: Flora of Ethiopia and Eritrea (1989-2009).

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Introduction

Tropical montane forests are among the most species-rich ecosystems on earth (Bussmann 2004; Mutke & Barthlott 2005). They are under severe land-use pressure worldwide, because the same environmental conditions that foster high species diversity also render tropical montane forest areas suitable for agricultural uses (Rodrigues et al. 2004; Burgess et al. 2007a; Cordeiro et al. 2007).

Knowledge of the spatial pattern of biodiversity is crucial to assess the consequences of forest degradation and habitat loss caused by human activities, and to develop systematic conservation strategies (Haila & Margules 1996; Ferrier 2002; Dudley & Parish 2006; Fjeldså 2007). One particular challenge is to adequately capture changes in plant species diversity along altitudinal gradients (Hedberg 1969; Vázquez & Givnish 1998; Hemp 2006; Martin et al. 2007; Richter 2008). At present, floristic inventories and data on plant species distribution patterns are far from complete in many parts of the world.

The Afromontane areas of eastern Africa, including the Ethiopian highlands, constitute vivid examples of tropical forest ecosystems that have exceptional species richness, high concentrations of endemic species, and which are under great human land-use pressure. They are, therefore, internationally recognized as the Eastern Afromontane Biodiversity Hotspot (Mittermeier et al. 2004). In southwestern Ethiopia, where the Bonga region is located, 40% of the forests have been modified or destroyed since the 1970s by new settlements, agricultural activities and timber extraction (Reusing 2000). These forests are of particular value because they belong to the centre of origin and genetic diversity of Arabica coffee *Coffea arabica* and still harbour wild populations of this species. Conservation planning measures aiming to reconcile forest use and conservation, for example, in the form of a biosphere reserve (UNESCO 2008), require data on the floristic diversity of the forests, including the distribution of wild coffee.

The forest types and plant species distribution within the Eastern Afromontane Biodiversity Hotspot are relatively well known for the Eastern Arc Mountains in Kenya and Tanzania (Lovett 1988; Lovett 1993; Lovett & Wasser 1993; Newmark 2002; Burgess et al. 2007b). In contrast, the Ethiopian montane forests have so far been described mainly on the basis of herbarium specimens or qualitative field observations (Logan 1946; Pichi-Sermolli 1957; von Breitenbach 1963; Greenway 1973; Friis 1986, 1992; Friis & Demissew 2001); few quantitative surveys exist (Woldemariam 2003; Senbeta et al. 2005). Friis (1992) classified the forest vegetation of southwestern Ethiopia at altitudes between 1500 m and 2600 m as the wetter type of moist Afromontane forest and between 500 m and 1500 m as transitional rainforest. Other studies divided montane forest into lower montane (1200-1800 m) and upper montane (> 1800 m) forest (Lovett 1993; Iremonger et al. 1997).

The objective of this study was to quantify the relationships between altitude and plant species distribution in the forests of the Bonga region. Based on the findings of the aforementioned works, we hypothesized that altitudinal variations in the moist montane forest vegetation of southwestern Ethiopia can be systematically identified and statistically demonstrated. The results were expected to inform further development of the Ethiopian forest classification and to support conservation planning in the Bonga region.

Methods

Study area

The study region is located in the mountainous highlands west of the Great Rift Valley and situated near the town of Bonga, the administrative centre of the Kaffa zone, Southern Nations Nationalities and Peoples Regional State (SNNPRS) (Fig. 1). It

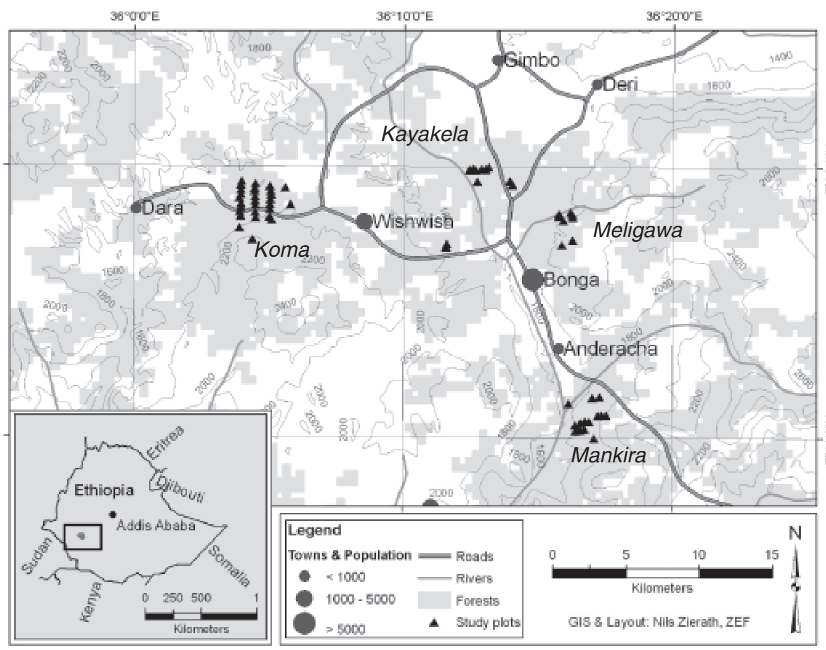

Fig. 1. Location of the Bonga region (SW Ethiopia), the forest fragments studied at Mankira, Kayakela, Meligawa and Koma, and the corresponding study plots.

consists of a mosaic of forest, agricultural fields, grassland and built-up areas. Part of the forest is the Bonga National Forest Priority Area (NFPA), which was demarcated in 1985 and further expanded in 2002. However, implementation of the NFPA, including a ban on forest degradation and deforestation, has been weak and the forest areas are under increasing land-use pressure (Reusing 2000; Bekele 2002).

The landscape is dissected by numerous small streams and has a highly diverse topography with flat plateaus, undulating to mountainous terrain and very steep slopes with an inclination of up to 60%. Altitude ranges from 1450 m to 2370 m. The most common soils under forest are nitisols, but cambisols and regosols also occur. Soil acidity varies between pH (H_2O) 4.1 and 6.3. Generally, the soils are rich in organic matter, have a medium to high total nitrogen and exchangeable potassium content, and are low in available phosphorous. They are well drained and have good water-holding capacity.

The Bonga region is humid and, according to the Koeppen classification, has a warm tropical rainy climate (Liljequist 1986). The rainfall is unimodal with low rainfall from Nov to Feb, and the wettest months between May and Sep. The coolest months are Jul and Aug in the middle of the main rainy season, while the hottest months are Feb to May.

Climate data for the study region were provided by the meteorological stations of Bonga (7.13° N, 36.17° E; 1725 m) and Wishwish (7.16° N, 36.11° E; 1950 m) (source: Ethiopian Meteorological Service Agency 1953–2001). The mean annual temperature at Bonga is 19.2°C, and the mean annual rainfall 1723 mm yr^{-1}, with high variations from year to year (1259–2569 mm yr^{-1}). In Wishwish, the mean annual temperature is 18.5°C and the mean annual rainfall is 1794 mm yr^{-1}, ranging from 1356 mm yr^{-1} to 2445 mm yr^{-1}.

Vegetation survey

Preliminary field investigations carried out at Bonga in March 2003 identified four forest fragments with relatively undisturbed natural forest vegetation (i.e., low human impact and undisturbed vegetation structure with dense canopy cover and a shaded understory). Vegetation surveys were carried out in these forest areas between May 2003 and Jan 2005, employing a total of 62 study plots (20 m×20 m). Sampling had to be suspended between mid-Jun and mid-Oct each year because of heavy rains, but no seasonal changes in the species composition of the forest were observed.

Although the number of study plots in each forest fragment varied according to the size of the fragment (Table 1), the study plots were equally distributed across the altitudinal gradient to avoid sampling artefacts (Fig. 2). Plots were located every 300 m along transects. These transects were spaced 1 km apart, or placed deliberately in order to capture a representative variety of forest aspects.

Vascular plant species were identified according to the Flora of Ethiopia and Eritrea (1989-2009), the Flora of Tropical East Africa (1996 and continuing), and by comparison with correctly identified specimens kept at the National Herbarium in Addis Ababa, Ethiopia, and the Herbarium of the Royal Botanic Gardens, Kew, UK. The Flora of Ethiopia and Eritrea was used as the nomenclatural authority.

Species of the herb layer were recorded as presence–absence data. For woody plants and woody and herbaceous climbers, height and diameter at breast height (DBH) were measured if height ≥ 0.5 m or DBH ≥ 2 cm.

Table 1. Size, plot number, protection status and altitude of the forest fragments studied. NFPA = National Forest Priority Area.

Forest fragment	Mankira	Kayakela	Meligawa	Koma
Size (ha)	1100	700	600	1700
Number of study plots	14	11	8	29
Protection status	NFPA	–	NFPA	NFPA
Altitudinal range of plots (m)	1600–1810	1620–1750	1710–1880	1830–2280

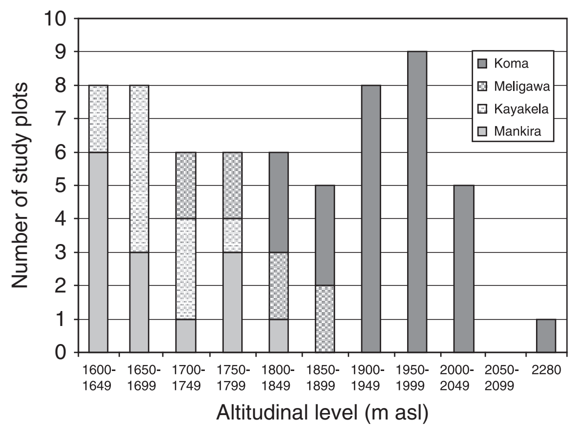

Fig. 2. Altitudinal distribution of the study plots in the four forest fragments at Mankira, Kayakela, Meligawa and Koma.

Woody plant and climber species were assigned to five different categories based on growth forms (Jacobs 1981; Ewel & Bigelow 1996; Mueller-Dombois & Ellenberg 2002). Distinctions were made according to field observations and specimen descriptions in the Flora of Ethiopia and Eritrea, as follows: shrub – woody plants having several stems arising from the base and lacking a single trunk, usually <5 m tall; small tree – woody plants with a single trunk reaching a maximum height of 15 m, including *Dracaena* species and *Cyathea manniana* (tree fern); tall tree – woody plants with one main trunk and a distinct and elevated head growing taller than 15 m, including *Phoenix reclinata* (palm); woody climber – climbing plants with a woody stem (synonym: liana); herbaceous climber – climbing plants without a woody stem.

Site factors

For each study plot, altitude, inclination (slope) and moss cover were recorded. Moss cover was assumed to be an indicator of long-term site humidity, because dense moss layers on trees, as well as abundant moss festoons, are usually observed in highly shaded and humid parts of forest (Jacobs 1981; Taylor 1999). Moss festoons are mosses that hang down from branches and reach lengths from 5 to 20 cm and more. Identification of moss species was not possible; however, based on visual inspection, the same species were present throughout the forest.

Moss cover for each study plot was calculated as follows:

$$\text{Moss cover} = \left[\frac{(\%\text{-trees}) \times (\%\text{-trunk cover})}{100}\right] + \left[\frac{(\%\text{-trees}) \times (\%\text{-festoons})}{100}\right] / 2$$

where %-trees = the estimated percentage of woody plants (dbh >2 cm) in the plot with moss present, %-trunk cover = the estimated average percentage of moss cover on the trunks and branches of these woody plants, and %-festoons = the estimated percentage of these woody plants with moss festoons.

Data analysis

Species composition was analysed with ordination techniques, using CANOCO version 4.52 and CANODRAW version 4.12 (Microcomputer Power, Ithaca, NY, USA). Indirect (unconstrained) gradient analysis was employed to display study plots within the multidimensional ordination space based on similarities in species composition. In the case of indirect analysis, the ordination axes are theoretical gradients, and the environmental data are subsequently used to interpret the ordination. Initial tests with detrended correspondence analysis (DCA) indicated a linear rather than unimodal response of the data. Therefore, a linear model – a principal component analysis (PCA) – was selected (ter Braak & Šmilauer 2002; Lepš & Šmilauer 2003).

The PCA was performed separately for woody plants and climbers, and for the herb layer species. For the former, the PCA was based on abundance data considering species with more than one individual, whereas in the case of the latter the analysis used presence–absence data considering species observed in at least two study plots. Abundance data were log transformed to account for the large differences in species abundances. Ordination diagrams were most coherent when species data tables were standardized by samples and centred by species.

T-value biplots were used to identify the site factors that can, on their own, explain a significant amount of variation for individual species. These ordination diagrams are based on reduced-rank regression, combining multiple regressions between species abundances and a particular site factor, and the model defined by the PCA. Arrows represent species, and the site factor is displayed as a solid symbol. The interpretation of reduced-rank regression biplots is facilitated by so-called Van Dobben circles, which enclose the species arrows of those species that react significantly to the factor tested (t-value $<|2|$) (ter Braak & Looman 1994). Species positively correlated with the respective site factor are enclosed by the positive circle (i.e., circle adjacent to the arrow tip of the environmental variable), while the arrow tips of species with a negative correlation are enclosed by the negative (mirror) circle.

Indicator species analysis was performed with PC-ORD (version 5.0; MjM Software, Gleneden Beach, OR, USA) to evaluate the importance of woody plants and climbers at two different altitudinal levels. This method combines information about exclusiveness, (i.e., the proportional abundance) and faithfulness (i.e., proportional frequency) of species in a particular group. Statistical significance was tested using Monte Carlo randomization procedures (number of runs = 4999). Only woody species and climbers with more than one individual were considered. Indicator values vary from zero (no indication) to 100% (perfect indication). A threshold level of 25% was chosen for the indicator value, assuming that a characteristic (indicator) species is present in at least 50% of one site group, and that its relative abundance in that group reaches at least 50% (Dufrêne & Legendre 1997).

Whittaker's three kinds of diversity were calculated for woody plants and climbers and for herb layer species for each forest fragment (McCune & Grace 2002): α-diversity as average species richness per plot (= species density); β-diversity as a measure of heterogeneity calculated on the basis of the ratio of the total number of species to the average number of species (γ over α); and γ-diversity as landscape-level diversity (i.e., the total number of species across plots). The significance of variations in α-diversity between fragments was tested with the one-way ANOVA and Bonferroni test[s] (*post hoc*) in SPSS (version 13.0; SPSS Inc., Chicago, IL, USA). Shannon's diversity index $[(H') = -\Sigma^{i=1/s} \rho_i \times \ln \rho_i]$ and Shannon's evenness $[(E) = H'/\ln$ (number of species)] were calculated for each fragment using presence–absence data (herb layer species) and abundance data (woody plants and climbers) (Magurran 1988). Diversity measures facilitate the comparison of species distribution patterns between sites; however, they need to be carefully interpreted because of their sensitivity to sample size, which is most pronounced in species richness measures (Peet 1975; Smith & Wilson 1996; McCune & Grace 2002).

Results

A total of 220 plant species were recorded in 62 study plots: 80 herb layer species and 140 woody species and climbers. Few species were ubiquitous and occurred in more than 80% of all study plots (i.e., 8% of the herb layer species and 11% of the woody plants and climbers). Frequent woody species were mostly small trees and woody climbers, which also had high abundances (see the Supporting Information, Appendix S1). The majority of species, however, were unequally distributed among study plots. Moreover, gradual changes in species composition along the altitudinal gradient were observed.

In the following, the results of the analysis of the woody plants and climbers and the herb layer species are presented separately because abundance data were recorded for the former, but presence–absence data for the latter.

Woody plants and climbers

Altitude was strongly associated with species composition, as indicated by the long arrow in the ordination diagram (Fig. 3). The arrow points to the right side of the diagram, where all study plots above 1830 m are depicted. The diagram also demonstrates a positive correlation between precipitation and altitude, as the arrow for moss cover, an indicator of humidity, points in the same direction as the altitudinal arrow. The eigenvalues (λ) and the cumulative percentage of explained variance of species data were low (Table 2). This is, however, common for ecological field data and does not complicate the interpretation of the results (Økland 1999; ter Braak & Šmilauer 2002; Lepš & Šmilauer 2003).

Although the plots are continuously scattered along the altitudinal arrow (Fig. 3), the clear separation of plots situated above and below 1830 m suggests the definition of two subgroups: (1) study plots located between 1830 m and 2280 m, called upper montane forest type and found mainly at Koma, and (2) study plots located between 1600 m and 1830 m, called lower montane forest type and located mainly at Kayakela and Mankira.

The importance of the altitudinal gradient is underlined by the fact that the distribution of many species was significantly correlated with altitude. The *t*-value biplot shows species significantly positively correlated with altitude within the positive response area, and species with a significantly negative correlation in the negative response area (Fig. 4).

Using the threshold level of 1830 m as the grouping variable for the study plots, the indicator species analysis demonstrated that species significantly correlated with altitude in the *t*-value biplot were also significant indicator species (i.e., they were characteristic of one of the forest types; Table 3). They may have been present in the other type but were less abundant there (Appendix S1).

Upper montane forest was characterized by the common tall tree species *Elaeodendron buchananii*, *Syzygium guineense* and *Ilex mitis*. Typical species of the understory were *Psychotria orophila*, *Canthium oligocarpum*, *Galiniera saxifraga* and *Lepidotrichilia volkensii* (Table 3). The tall tree *Trilepisium madagascariense* was a distinct indicator species of lower montane forest rare in the upper montane forest type, while *Dracaena fragrans*, *Vepris dainelli* and *C. arabica* were typical understory species. Some of the species that were restricted to either lower montane forest, such as *Psychotria peduncularis* and *Albizia grandibracteata*, or upper montane forest, such as *Urera hypselodendrum*, provided no significant results in the statistical analyses, because too few individuals were sampled (Appendix S2).

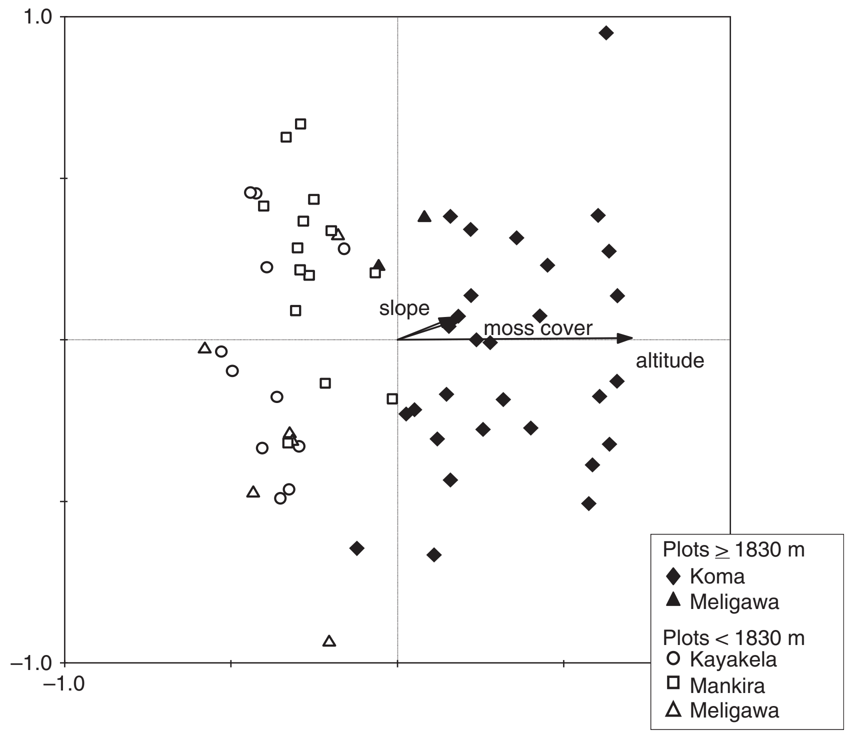

Fig. 3. Ordination of study plots at four forest fragments according to the abundance data of woody plants and climbers (principal component analysis, PCA) based on 124 species with more than one individual; data were log transformed. Arrows represent site factors with the value of the factor continuously increasing in the arrow direction; the longer the arrow, the more strongly associated that factor is with species composition.

Table 2. Results of the principal component analysis (PCA) for woody plants and climbers (abundance data, 124 species with more than one individual) and the herb layer vegetation (frequency data, 52 species present in at least two study plots); 62 study plots.

	Axes: 1	2	3	4
Woody plants and climbers				
Eigenvalues (λ)	0.141	0.070	0.058	0.052
Species-environment correlations	0.784	0.112	0.146	0.624
Cumulative % variance of species data	14.1	21.1	26.9	32.1
Cumulative % variance of species–environment relation	57.6	58.2	59.0	72.5
Herb layer vegetation				
Eigenvalues (λ)	0.109	0.088	0.079	0.071
Species-environment correlations	0.495	0.688	0.168	0.218
Cumulative % variance of species data	10.9	19.7	27.5	34.7
Cumulative % variance of species–environment relation	24.8	63.6	65.7	68.8

Diversity measures further illustrated differences in species distribution patterns between forest fragments. Koma, representing the upper montane forest type, exhibited the highest species richness and Shannon index for all woody plant and climber species, which may have been related to the large sample size at this forest fragment. However, partial analysis of the different growth forms revealed that the Shannon index for tall tree species was highest at Mankira (Table 4). Moreover, and despite the differences in sample size, tree species richness in the upper canopy (tall trees with a height greater than 15 m) was also highest at Mankira. The relatively high Shannon index for the upper canopy in this forest fragment can be attributed to the even distribution of species abundances. At Mankira, four tree species constituted 50% of all canopy individuals: *T. madagascariense* (17%), *Sapium ellipticum* (13%), *Schefflera abyssinica* (13%) and *Olea welwitschii* (12%). At Koma, three species made up 50 % of the canopy individuals: *O. welwitschii* (22%), *E. buchananii* (17%) and *S. guineense* (14%).

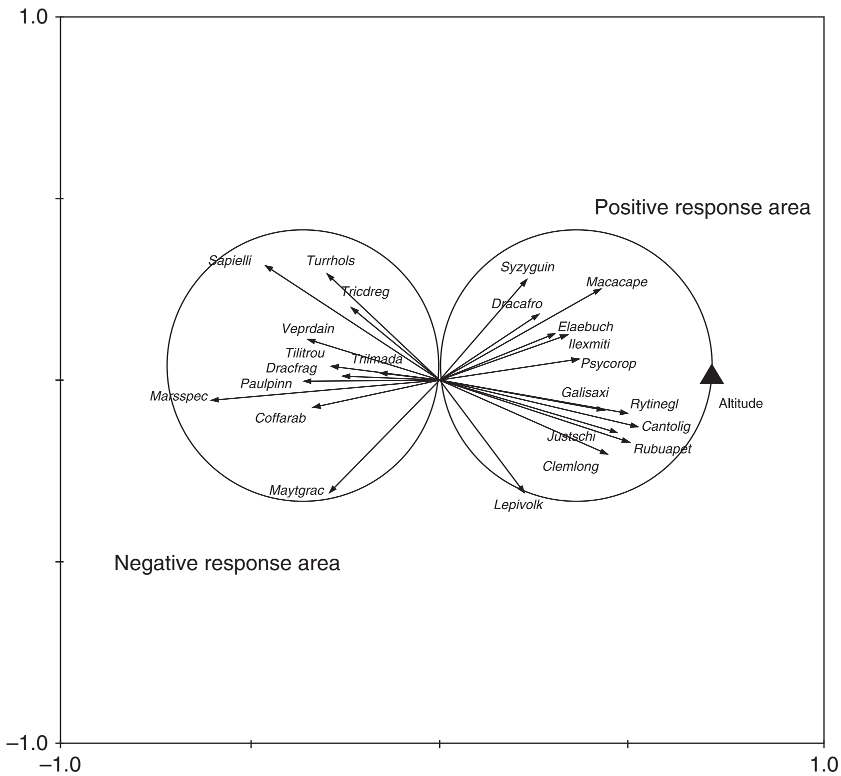

Fig. 4. *T*-value biplot with Van Dobben circles based on multiple regressions between abundances of woody species and climbers and the site factor 'altitude', and taking into account the model generated by principal component analysis (PCA) (Fig. 3). Arrows represent species, and the site factor is displayed as a solid symbol. Only those species with a significant response to altitude are depicted (first four letters of the generic name followed by first four letters of the species name); full names are given in Table 3. Species positively correlated with altitude are enclosed by the positive response area (i.e., Van Dobben circle adjacent to the arrow tip of the environmental variable), while those with a negative correlation have their arrow tips enclosed by the negative response area.

Kayakela had the lowest Shannon index for the upper canopy because *T. madagascariense* alone represented 50% of the canopy individuals. Meligawa was not considered because of the small sample size at this fragment.

It is noteworthy that Mankira and Kayakela, both representing the lower montane forest type, had the same total species richness, but evenness and the Shannon index were much lower at Kayakela than at Mankira because of the extremely high abundance of *C. arabica* (small tree) and the dominance of *T. madagascariense* among the tall trees, as was mentioned above. The average species density (α-diversity) was significantly higher at Mankira than at Kayakela (Table 4).

Herb layer

The ordination diagram for herb layer species illustrates the influence of the different environmental factors on the species composition of the study plots (Fig. 5). Plots in the lower left corner of the diagram were located above 1830 m and had high moss cover, suggesting higher humidity. Most of these plots were situated in upper montane forest at Koma, which was characterized by high fern species richness. Of the 19 fern species found there, 12 were not encountered in any other forest fragment.

Plots in the upper left corner of the diagram were also humid, but situated at altitudes below 1830 m. They were mostly located in lower montane forest at Mankira and were characterized by many herb species not observed in other fragments, such as *Brillantaisia grotanellii* and *Leptaspis zeylanica* (Appendix S2). Plots in the upper right corner of the diagram were mostly below 1830 m and relatively dry. *Piper umbellatum* and *Aframomum zambesiacum* were characteristic of lower montane forest.

In contrast to the ordination for woody species and climbers (Fig. 3), the arrow for moss cover was not correlated with the arrow for altitude and it was

Table 3. Indicator species for upper montane forest (1830–2280 m) and lower montane forest (1600–1830 m) based on 124 woody plants and climbers with more than one individual, and 31 study plots for each forest type. Limits: indicator value (IV) > 25%, *P*-value < 0.05. Nomenclature: Flora of Ethiopia and Eritrea (1989–2009). [1]AfrM/e = Afromontane endemic, AfrM/n-e = Afromontane near-endemic, Sub-AfrM/n-e = sub-Afromontane near-endemic, GC-ZI-SZfr = Guineo-Congolian–East African forest belt linking species (Friis 1992).

Species	Family	Growth form	Distribution type[1]	IV	*P*-value
Indicator species for upper montane forest (1830–2280 m)					
Galiniera saxifraga	Rubiaceae	Small tree	AfrM/e	84	0.002
Psychotria orophila	Rubiaceae	Small tree	AfrM/e	84	0.000
Dracaena afromontana	Agavaceae	Small tree	AfrM/e	74	0.000
Elaeodendron buchananii	Celastraceae	Tall tree	AfrM/n-e	71	0.000
Canthium oligocarpum	Rubiaceae	Small tree	AfrM/e	67	0.001
Syzygium guineense ssp *afrom.*	Myrtaceae	Tall tree	AfrM/n-e	67	0.001
Lepidotrichilia volkensii	Meliaceae	Small tree	AfrM/e	66	0.001
Rytigynia neglecta	Rubiaceae	Shrub	-	66	0.000
Justicia schimperiana	Acanthaceae	Shrub	-	42	0.003
Macaranga capensis	Euphorbiaceae	Tall tree	AfrM/n-e	41	0.005
Ilex mitis	Aquifoliaceae	Tall tree	AfrM/n-e	36	0.000
Rubus apetalus	Rosaceae	Shrub	-	30	0.009
Clematis longicauda	Ranunculaceae	Woody climber	-	29	0.001
Indicator species for lower montane forest (1600–1830 m)					
Trilepisium madagascariense	Moraceae	Tall tree	GC-ZI-SZfr	97	0.000
Dracaena fragrans	Agavaceae	Small tree	GC-ZI-SZfr	82	0.000
Tiliacora troupinii	Menispermaceae	Woody climber	-	75	0.000
Coffea arabica	Rubiaceae	Small tree	AfrM/e	73	0.002
Vepris dainellii	Rutaceae	Small tree	AfrM/e	71	0.000
Maytenus gracilipes	Celastraceae	Shrub	-	67	0.001
Paulinia pinnata	Sapindaceae	Woody climber	-	61	0.000
Trichilia dregeana	Meliaceae	Tall tree	Sub-AfrM/n-e	53	0.000
Turraea holstii	Meliaceae	Shrub	AfrM/e	45	0.000
Sapium ellipticum	Euphorbiaceae	Tall tree	GC-ZI-SZfr	38	0.018
Marsdenia ssp.	Asclepiadaceae	Woody climber	-	32	0.001

Table 4. Species diversity patterns for woody plants and climbers in the forest fragments.*Significantly higher at Mankira than at Kayakela (*P* < 0.05, Bonferroni test, one-way ANOVA).

	Mankira	Kayakela	Meligawa	Koma
Number of study plots	14	11	8	29
Altitude (m)	Below 1830	Below 1830	Intermediate	Above 1830
Humidity (moss cover)	High	Low	Low	High
Results for all woody plant and climber species				
Species richness (γ-diversity)	87	87	74	114
Species density (α-diversity)*	45.1	38.4	40.4	42.0
β-diversity (γ/α)	1.93	2.27	1.83	2.71
Evenness	0.65	0.55	0.61	0.70
Shannon index	2.89	2.44	2.63	3.30
Partial results for tall tree species				
Species richness (γ-diversity)	32	33	28	34
Shannon index	2.84	2.50	2.69	2.79
Partial results for tall tree species in the upper canopy (height > 15 m)				
Species richness (γ-diversity)	20	18	13	18
Shannon index	2.59	1.92	2.39	2.32

longer (i.e., more strongly associated with species composition). This ordination also shows a greater overlap in the distribution of plots above and below 1830 m (Fig. 5). As no single gradient dominated the distribution pattern of the herb layer species, the *t*-value biplot and indicator species analyses are not presented.

The difference in the herb species composition between the forest fragments was also apparent in the species diversity patterns. Species richness and Shannon index were highest at Koma because of a larger number of rare species (Appendix S2), which could be a consequence of the large sample size (Table 5). In the case of Mankira and Kayakela, both representing lower montane forest, the sample size was similar but Mankira had a much higher diversity in terms of species richness, species density and Shannon index.

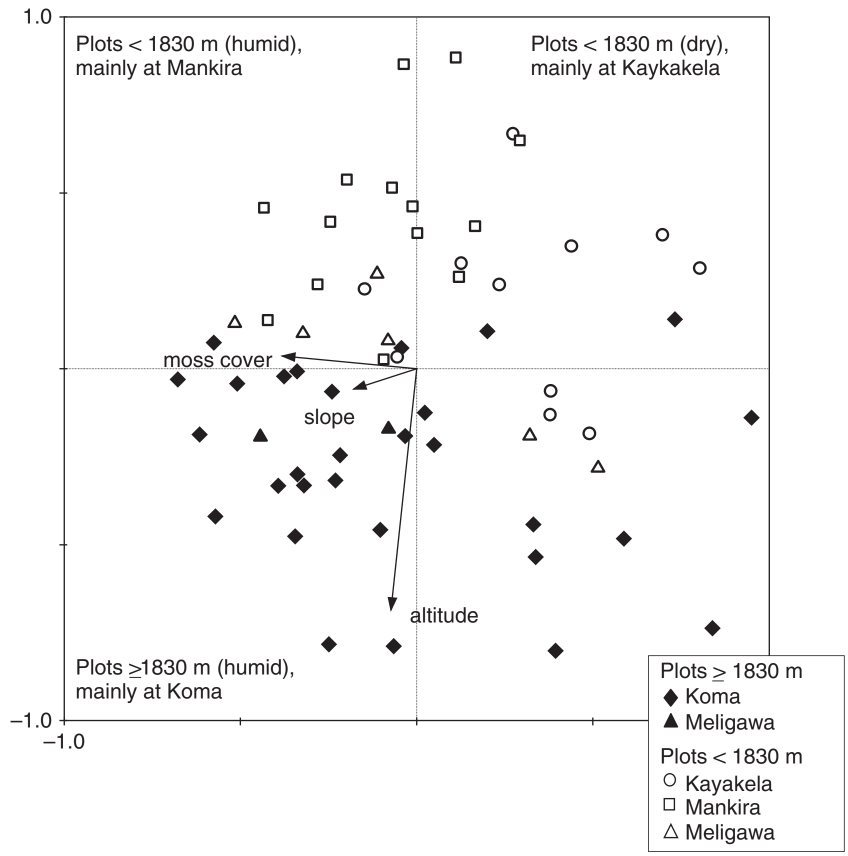

Fig. 5. Ordination of study plots in the four forest fragments according to species frequency data for the herb layer vegetation (principal component analysis, PCA) based on 52 species occurring in at least two study plots. Arrows represent site factors with the value of the factor continuously increasing in the arrow direction; the longer the arrow, the more strongly associated that factor is with species composition.

Table 5. Species diversity patterns for herb layer vegetation in the forest fragments. *Significantly higher at Mankira than at Koma and Kayakela ($P < 0.05$, Bonferroni test, one-way ANOVA).

	Mankira	Kayakela	Meligawa	Koma
Number of study plots	14	11	8	29
Altitude (m)	Below 1830	Below 1830	Intermediate	Above 1830
Humidity (moss cover)	High	Low	Low	High
Species richness (γ-diversity)	43	27	33	61
Species density (α-diversity)*	18.3	12	15.5	14.9
β-diversity (γ/α)	2.35	2.25	2.13	4.16
Evenness	0.91	0.91	0.93	0.85
Shannon index	3.43	3.00	3.25	3.49

Discussion

Our results with regard to species composition suggest that the forests in the Bonga region belong to the wetter type of moist Afromontane forest as described previously for southwestern Ethiopia (Friis 1992). The upper canopy (15-40 m) is composed of species such as *O. welwetschii*, *S. abyssinica*, *Milletia ferruginea*, *P. reclinata*, *Polyscias fulva*, *Pouteria adolfi-friederici* and *Ocotea kenyensis*. In the lower canopy (< 15 m high), species such as *Chionanthus mildbraedii*, *Rothmannia urcelliformis*, *Oxyanthus speciosus*, *Deinbollia kilimandscharica* and *Teclea nobilis* are widespread (Appendix S1).

Moreover, the results also demonstrate gradual changes in species composition with altitude that were not noted by earlier vegetation surveys carried out in the region (Friis et al. 1982; Ersado 2001; Kelbessa & Soromessa 2004). The continuous nature of change in moist forest communities is related to a continuous change in environmental variables along the altitudinal gradient (i.e., precipitation and temperature) (Lovett 1993). These two factors might reach a threshold level at around 1830 m in the Bonga region, as is suggested by the difference in species composition of the study plots located above and below this altitude (Fig. 3). This supports our hypothesis that altitudinal variation in species composition can be identified and statistically demonstrated for the moist montane forest vegetation of southwestern Ethiopia.

Accordingly, we propose two forest types for the Bonga region: (1) upper montane forest above 1830 m, and (2) lower montane forest below 1830 m. The two forest types are characterized by statistically significant indicator species (Fig. 4, Table 3), and can easily be recognized in the field by the presence of *T. madagascariense* in the canopy layer of lower montane forest. Indicator species (Table 3) and tree species diversity in the upper canopy (Table 4) underline the notion that forests between elevations of 1525 and 1830 m harbour more phytogeographic elements and are richer in tree species than forests situated between 1830 m and 2135 m (Friis 1992).

Most indicator species occur over a wider altitudinal range but are most frequent and abundant within only one of the forest types (Appendix S1), presumably representing their ecological optimum (Mueller-Dombois & Ellenberg 2002; Austin 2005). Thus, the shift in species composition at around 1830 m does not justify the definition of a floristic critical altitude in the strict sense: i.e., ''altitudes or narrow altitudinal bands within which a substantially greater number of species reach either the upper or lower limits of their ranges than in the intervening intervals'' (Hamilton 1975).

Our study supports the notion of the importance of altitude as one of the main determinants of plant species distribution patterns in tropical forests, as was shown for other parts of eastern Africa (Hamilton 1975; Eilu et al. 2004). Lovett (1993) also identified the altitude of 1800 m as a threshold level for floristically different montane forest types in the Eastern Arc Mountains of Tanzania. Similar to the Bonga region, fern diversity reaches a maximum in montane forests above 1800 (-2400) m at Mount Kilimanjaro, clearly indicating increased precipitation above this altitude (Hall & Swaine 1976; Hemp 2001). However, altitudinal threshold levels can vary between different geographic regions, as the lower level of cloud or mist zones depends on interactions between topography and atmospheric flows (Bussmann 2006; Hemp 2006).

Species of the herb layer were probably more strongly influenced by smaller-scale environmental variations than woody plants and climbers. For example, Mankira and Kayakela, the two forest fragments with lower montane forest shared most woody plant and climber species but differed in terms of their herb layer vegetation. We assume that the composition of the herb layer was determined not only by variations in humidity caused by the altitudinal gradient, but also by local variations in humidity caused by other factors such as exposure or small streams because the arrows for moss cover and altitude were not correlated in the ordination diagram (Fig. 5). A vegetation study from southeastern Ethiopia also suggests that herb layer species react to small-scale changes in environmental conditions, while woody plant and climber composition is more likely to be governed by changes on a larger scale (i.e., mainly altitude; Woldu et al. 1989). In addition, the differences in forest humidity might be the reason for the generally higher species diversity at Mankira than at Kayakela (Table 5).

The distinction between lower and upper montane forest types underlines that forests need to be protected along the whole length of the altitudinal gradient in order to preserve the particular plant species diversity of the Bonga region. Consideration of the entire range of elevations has also been recommended for conservation planning in other regions of the Eastern Afromontane Biodiversity Hotspot (Lovett et al. 2001; Hall et al. 2009).

Owing to forest fragmentation, however, there is no single site at Bonga where natural forest could be protected along its entire altitudinal range. Following the principle of complementarity (Margules et al. 2002), we therefore recommend a multi-site approach (i.e., the establishment of at least two protected areas that cover forest fragments at low altitude and at high altitude, respectively). Although the areas in the Bonga region with remaining natural forest are rather small, e.g. 1300 ha at Koma (upper montane forest) and 700 ha at Mankira (lower montane forest), our study shows that these forest fragments have been able to maintain a particular species composition. The protection of smaller forest patches that can act as species refugia or stepping stones is considered to be a crucial contribution to the conservation of floristic diversity in tropical forests, particularly in the face of the potential threat posed by global climate change (Gentry 1992; Turner & Corlett 1996; Schwartz 1999; Heller & Zavaleta 2009).

The implementation of relatively small protected areas for forests at different altitudes can only be successful if embedded in an overarching conservation and development concept. This could be achieved within the framework of a biosphere reserve (UNESCO 2008), a proposal for which is currently being developed by a group of Ethiopian and German stakeholders. They envision the designation of several core areas for forest conservation, which are surrounded by buffer zones of managed forest, in order to reconcile forest use and conservation in the highly populated Bonga region (Senbeta et al. 2008; GTZ 2008). The prospective biosphere reserve could be integrated with the existing NFPA; however, the weak conservation status of the latter underlines the fact that consideration of developmental issues and strong support from local to national levels will be necessary for successful implementation.

Using wild coffee, *C. arabica*, as a flagship species at the international level could help in the creation of conservation awareness and action for the Ethiopian Afromontane forests (Noss 1999). However, concentrating on *C. arabica* when designating protected areas for biodiversity conservation (i.e., putting more emphasis on forest areas where wild coffee is more abundant) would only inadequately capture overall species diversity. This is especially so because the results of the study did not indicate whether the high abundance of *C. arabica* in lower montane forest is caused by favourable environmental conditions or is the result of human management interventions that have taken place in the region over centuries (Strenge 1956; Meyer 1965). This underlines the need for caution when using flagship species (van Jaarsfeld et al. 1998; Andelman & Fagan 2000). Experience from other hotspot regions shows that, ideally, conservation planning should employ a multitaxonomic approach (Hacker et al. 1998; Kremen et al. 2008).

In addition to informing regional conservation planning, our results can contribute to the refinement of the Ethiopian forest classification system. To date, the lower limit of moist Afromontane forest has been assumed to be 1500 m, below which it is replaced by transitional rainforest between 500 m and 1500 m (Friis 1992). Many of the species that are reported to be restricted to this transitional forest, such as *D. fragrans*, *E. buchananii*, *Eugenia bukobensis*, *P. reclinata*, *Trichilia dregeana*, *T. madagascariense* and *V. dainellii*, also occur above the critical altitude of 1500 m in the Bonga region. Therefore, we suggest further investigation into the lower limit of lower montane forest and a revision of the transitional forest zone as currently described for Ethiopia.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Abundance and relative abundance of woody species and climbers at six altitudinal levels; relative abundance: number of individuals of a species at an altitudinal level relative to the total number of individuals occurring at that altitude. Nomenclature: Flora of Ethiopia and Eritrea (1989-continuing).

Appendix S2. Frequency of herb layer species in all study plots (total) and in the forest fragments at Koma, Mankira, Kayakela and Meligawa; for the relationship between species composition and environmental variables, refer to Fig. 4. Nomenclature: Flora of Ethiopia and Eritrea (1989-continuing).

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