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Both forest fragmentation and coffee cultivation negatively affect epiphytic orchid diversity in Ethiopian moist evergreen Afromontane forests



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ABSTRACT

The moist evergreen Afromontane forest of SW Ethiopia has become extremely fragmented and most of the remnants are intensively managed for cultivation of coffee (Coffea arabica), with considerable impacts on forest structure, biodiversity and ecosystem functioning. We assessed the effect of coffee forest management and forest fragmentation on epiphytic orchid diversity. We selected large and small intensively managed forest sites and compared their epiphytic orchid diversity with the diversity of natural unfragmented forest. We surveyed 339 canopy trees using rope climbing techniques. Orchid richness decreased and community composition changed, from the natural unfragmented forest, over the large managed forest fragments to the small managed forest fragments. This indicates that both forest management and fragmentation contribute to the loss of epiphytic orchids. Both the removal of large canopy trees typical for coffee management, and the occurrence of edge effects accompanying forest fragmentation are likely responsible for species loss and community composition changes. Even though some endangered orchid species persist even in the smallest managed fragments, large forest fragments are better options for the conservation of epiphytic orchids than small forests. Our results ultimately show that even though shade coffee cultivation is considered as a close-to-nature practice and is promoted as biodiversity conservation friendly, it cannot compete with the epiphytic orchid conservation benefit generated by large unmanaged moist evergreen Afromontane forests.

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1. Introduction

Tropical forest landscapes have been subject to dramatic changes in terms of habitat loss and fragmentation (Foley et al., 2005; Lambin et al., 2003; Laurance, 2007), and a considerable part of the remaining forests has been converted into tree plantations or is strongly managed and disturbed (Dirzo and Raven, 2003; Gibson et al., 2011). Forest fragmentation poses a threat to plant populations, and ultimately to plant species richness, through the occurrence of genetic erosion, resulting from inbreeding, genetic drift and reduced gene flow within small and isolated populations (Honnay and Jacquemyn, 2007; Young et al., 1996). Furthermore, forest fragmentation may negatively affect pollinator abundance

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and diversity, as fragments can become too small to sustain pollinator communities, or too isolated to attract a large diversity of pollinators. This may jeopardize pollination efficiency and plant reproductive success, and therefore, ultimately also reduce plant species richness (Aguilar et al., 2006; Tscharntke and Brandl, 2004).

Next to changes in their size and spatial configuration, also the habitat quality of many tropical forests has become affected. First, a relative increase in edge habitat, typical of small and irregularly shaped fragments, has altered the microclimate in large parts, or even in the whole forest fragment (Gehlhausen et al., 2000; Pinto et al., 2010; Ramos and Santos, 2006). Second, many tropical forests have become strongly affected by human disturbance and forest management, especially in more densely populated areas (e.g., Aerts et al., 2011). Wood extraction through removal of canopy trees is very common and may have important consequences for the forest microclimate and for pollinator abundance and behavior, possibly affecting plant reproduction and species diversity (Benítez-Malvido and Martínez-Ramos, 2003; Eckert et al., 2010; Padmawathe et al., 2004).

Orchid epiphytes are important elements of tropical forest biodiversity (Haro-Carrión et al., 2009; Hietz, 2005) and can be



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expected to be very susceptible to the consequences of both forest fragmentation and forest disturbance for three reasons. First, epiphytic orchids are canopy dwelling organisms, often characteristic of large trees which are preferentially harvested during exploitation (Köster et al., 2009; Murren, 2002; Sodhi et al., 2008); second, these species typically depend on the specific forest micro-climate, characterized by high air humidity, low radiation and buffered temperature extremes (Larrea and Werner, 2010; Werner et al., 2005); third, they often rely on rather specialized pollinators that may be absent in highly managed or small and isolated forest fragments (Hietz, 1998; Murren, 2002). For these reasons, vascular epiphytes have been proposed as reliable indicators of overall forest ecosystem health and forest quality (Hietz, 1998; Nadkarni and Solano, 2002).

So far, the loss of epiphytic orchids has mainly been documented from disturbed and fragmented South and Central American forests (Haro-Carrión et al., 2009; Hietz, 2005; Köster et al., 2009; Moorhead et al., 2010), whereas data from tropical Africa are very limited (but see Hylander and Nemomissa, 2008). This highlights the need for more research in Africa, which sustains the second largest contiguous tropical forest in the world (Gibson et al., 2011). Additionally, the set-up of most studies does not allow disentangling the effects of forest fragmentation vs. forest management, as the smallest forest fragments are usually the most intensively managed (but see Köster et al., 2009). Here, we focus on the epiphytic orchid diversity of the remaining Ethiopian moist evergreen Afromontane forests. Most of these forests have become extremely fragmented through conversion of large forested areas into other land uses (Reusing, 2000). Furthermore, many of the remaining forests, where coffee (Coffea arabica) occurs as a natural understorey shrub, are intensively managed for coffee cultivation (Aerts et al., 2011; Schmitt et al., 2009).

The coffee cultivation intensity typically ranges from almost no interventions in the so-called forest coffee system (FC), to semiforest coffee (SFC) systems where the canopy layer is manipulated, shrubs are removed and the herbaceous understorey is cleared to reduce interspecific competition, and to increase coffee yield quality and quantity (Aerts et al., 2011: Labouisse et al., 2008). The SFC sites are generally dominated by early-successional species such as Croton macrostachys, Millettia ferruginea and Albizia gummifera while in the FC systems, the prevalent species are Afromontane rainforest late-successional species such as Prunus africana, Syzygium guineense and Olea welwitschii (Gole et al., 2008; Hundera et al., 2012) (Fig. D1). The SFC system in Ethiopia is somewhat similar to the rustic coffee system in Latin America where coffee shrubs were introduced under the original forest trees (Hernández-Martínez et al., 2009), though in Ethiopia coffee shrubs are naturally occurring in the understory and coffee populations are genetically more diverse (Aerts et al., 2012). As management in SFC forests mainly happens through removal of large canopy trees, it can be expected to be associated with the direct removal of suitable habitat for epiphytes, but also with changes in microclimate, because gaps in the canopy lead to rising air temperature, decreasing air humidity and increasing through-fall of rainwater (Acebey et al., 2003; Dietz et al., 2006).

The overall objective of this study was to assess the relative effects of coffee forest management vs. forest fragmentation on the species diversity and community composition of epiphytic orchids in Ethiopian moist evergreen montane forests. Therefore, we selected study sites that are intensively managed for coffee cultivation (SFC system) from both large forest remnants and from small forest remnants, and we compared their epiphytic orchid diversity with the diversity of natural, unmanaged continuous forests (FC system). Insights in the relative effects of forest fragmentation vs. forest management on epiphytic orchids may contribute to a more effective conservation strategy of this important species

group, and because of the indicator function of epiphytic orchids, it can provide important information with respect to general ecosystem health of Ethiopian moist evergreen Afromontane forests.

2. Materials and methods

2.1. Description of the study area

The study was performed in the Manna and Gera districts of the Jimma region in southwestern Ethiopia (Fig. 1). We selected 21 forest fragments that were strongly managed for coffee cultivation (SFC) from the Manna district. Six of these forests were large (5 fragments in the range of 14-24 ha; one fragment, Fetche, \sim 100 ha) (Large Managed Forest, LMF), and 15 were small (0.5-9 ha) (Small Managed Forest, SMF). In the SMF, 88 canopy trees were sampled for epiphytic orchids, while in the LMF 112 canopy trees were sampled. As a reference, 139 trees were surveyed in the continuous and undisturbed natural forest (>100,000 ha) of the Gera area (Large Natural Forest, LNF). To cover spatial variation in a similar way as in the fragmented forests, five forest blocks of ca. 5 ha were randomly established, at least 200 m from the forest edge, and the sampled trees were randomly selected from each block. The overall number of trees that were sampled across the three forest types totaled 339.

2.2. Field survey

Only large canopy trees standing well apart and separated from each other by at least 25 m were selected (Gradstein et al., 2003). These trees were expected to be richest in epiphyte species due to their large and highly diversified crowns, and because they have been longest available for colonization and establishment by epiphytes (Krömer and Gradstein, 2003). Double-rope climbing techniques (Fig. D2) and binoculars were used to survey the trees completely for the presence or absence of epiphytic orchid species. As an abundance measure of each species on each tree, we counted individual plants. Orchid species nomenclature and data on rarity and conservation status within Ethiopia were obtained from Demissew et al. (2004). Voucher specimens were collected in a digital herbarium (Appendix E). For each tree sampled, also the tree species, tree diameter at breast height (DBH (m)), tree height (m), and elevation (m a.s.l.) were recorded. Elevation was assumed to provide a good proxy for differences in local climatic conditions (mainly precipitation) between sampling points. To get a complete picture of the species richness, a plot of 10 m \times 10 m around each sampled tree was also surveyed for additional epiphytic orchid species that may be confined to the lower forest stratum (Gradstein et al., 2003). Because no orchid species could be found that were occurring in the plot and not in the central tree, all the reported analyses and results apply to the surveyed canopy trees.

2.3. Data analysis

For all trees, orchid species richness (*S*) and true diversity (the exponent of Shannon's diversity index or Hill's $N1 = e^{H'}$) (Hill, 1973; Jost, 2006) were calculated. Species turnover or beta diversity (β) was calculated for each forest type separately (LMF, SMF and LNF), as the total species richness divided by the average richness per tree (λ/α). We used EstimateS 8.2 (Colwell, 2009) (randomization without replacement, 500 runs) to perform sample based rarefaction (Mao Tau species accumulation curves) and to calculate incidendence-based estimations of species richness for each forest type (Chao2 and a first order Jackknife richness estimator). Non-metric multi-dimensional scaling (NMS) on the orchid abundance data was performed to quantify the orchid community

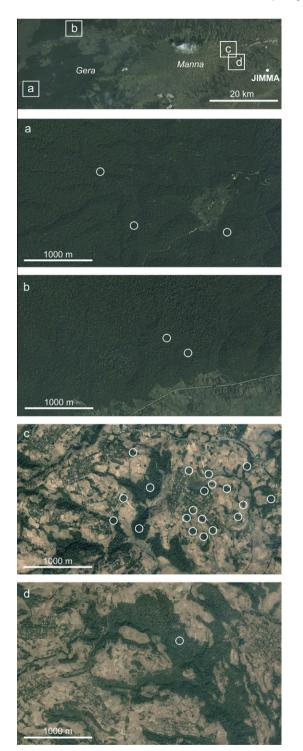


Fig. 1. Location of sampled moist evergreen Afromontane forest and forest fragments in Jimma zone, southwestern Ethiopia: (a and b) LNF: Large natural forests; (c) mixed SMF: Small managed forests and LMF: Large managed forests in Garuke; and (d) the LMF of Fetche. Satellite imagery ©2012 Cnes/SpotImage, Google, DigitalGlobe and GeoEye via GoogleEarth.

composition for each sampled tree. Additionaly, we used a multiresponse permutation procedure test (MRPP) and indicator species analysis (ISA) to determine multivariate differences between forest types and indicator species for each type. For the NMS we used the Sørensen distance measure, 50 runs with real data, 249 randomized runs, a stability criterion of 10^{-5} and a rotation for maximal variation. MRPP, ISA and NMS were performed in PC-ORD 5.31 (McCune and Mefford, 2006). To be able to statistically compare differences in *S*, *N*1 and community composition (NMS scores) between the three forest types (SMF, LMF and LNF), we had to account for the non-independency of the trees sampled within one forest fragment. Therefore, we applied linear mixed models for the dependent variables NMS1, NMS2 and *N*1 and a generalized mixed model with Poisson distribution and log link function for the dependent variable *S*, with Forest type as the only independent variable. To account for nonindependency of the sampled trees located within one forest fragment, or within one forest block in case of the LNF samples, Forest fragment or Forest block (for LNF) were included as a random factor in all models. The covariance structure for the random effect was left unstructured. Pairwise comparisons of the different species response variables between the three forest types were then performed using the least significant difference (LSD) test.

To get insight in the relative importance of the different recorded variables in mediating epiphyte richness and community composition, we re-ran the mixed models with Forest type, including four additional independent variables. These additional independent variables were Tree DBH, Tree height, Elevation and Tree type. Because of the high number of tree species (n = 33) and tree genera (n = 29) sampled, it was not possible to add 'species' or 'genus' as an independent factor in the models. Therefore, we defined Tree type as a categorical variable with two classes: earlysuccessional species (n = 177 trees; 11 species) and late-successional species (n = 162 trees; 22 species). We tested the main effects of all five independent variables, together with all their first order interactions. Model reduction occurred as follows: Non-significant interactions were first subsequently removed from the full models, followed by removal of non-significant main effects, leaving only non-significant main effects in the model when they were involved in a significant interaction. Pairwise comparisons of the different species response variables (S, N1, NMS1 and NMS2) between the three forest types were then performed using the least significant difference (LSD) test. These comparisons were based on marginal model means, i.e. keeping the other independent variables constant. All statistics, except the generalized mixed models. were performed using SPSS version 17 (SPSS Inc. 2008). The nonlinear mixed models were performed using the GLIMMIX procedure in SAS 9.2 (SAS Institute 2008).

3. Results

A total of 22 epiphytic orchid species belonging to eight genera were identified from the entire study area. These included 3 rare species; 13 species are listed as vulnerable, and four species (three restricted to LNF) are listed as endangered within Ethiopia (Appendix A). One terrestrial orchid species, Cynorkis kassneriana (Fig. D3), was also regularly recorded on branches, but as this study focused on true epiphytes, we omitted these records from the dataset. Out of the total 339 trees sampled, orchid species were present in 294 trees (86.7%). In total, we recorded 13,612 individuals and found on average 40 individuals and 2.85 species per tree (when including empty trees in the statistic). Overall, the LNF harbored more epiphytic orchids (20 species) as compared to SMF (9 species) and LMF (14 species) (Table 1). Eight (36%) of the identified species were confined to the LNF (Appendix A). The Mao Tao species accumulation curves started to flatten of after only relatively few of the trees (<50) were included (Fig. 2), and this for all three forest types. although less clear for the LMF. Richness estimators (Table 1) confirmed the presence of higher species richness in the LNF (ca. 22 species) compared to the managed forests (ca. 19 species in LMF; and ca. 10 species in SMF). There was a higher species turnover in the managed forest types (β diversity 11.2 in SMF; and 10 in LMF), as compared to LNF (β diversity 5.5) (Table 1). Three species, including the enigmatic Aerangis luteo-alba (Fig. D4), occurred in all

Table 1

Number of fragments and their dimensions, number of sampled trees, diversity indices and species richness estimation of epiphytic orchids in Ethiopian moist evergreen Afromontane forests: SMF: Small managed forests; LMF: Large managed forests; LNF: Large natural forests.

	SMF	LMF	LNF
Fragments/blocks	15	6	5
Average size of forest (ha)	4	50	>100,000
Altitudinal range (m.asl)	1965-2036	1873-2081	1869-2085
Trees sampled (with orchids)	88 (62)	112 (98)	139 (134)
Average tree height (m)	13.26	13.28	16.67
Average DBH (m)	0.78	0.75	0.76
% Trees with orchids	70	88	96
% Shrubs with orchids	91	83	83
Species richness per tree	1.96	2.2	4
Beta diversity	11.22	10	5.5
Total species richness	9	14	20
Average abundance per tree	15.4	32	62
Expected richness Jack1 (SD)	9.98 (1.0)	18.95 (2.6)	21.99 (1.4)
Expected richness Chao2 (SD)	9.0 (0.25)	23.9 (10.13)	20.5 (1.29)

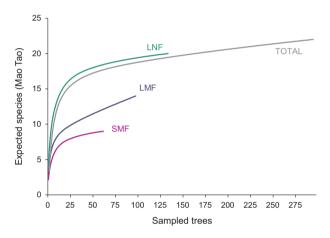
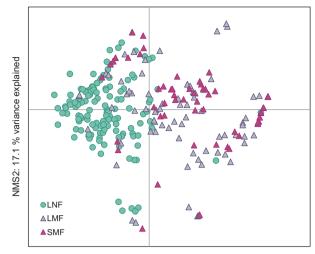


Fig. 2. Species accumulation curves: number of sampled trees against expected number of orchid species (Mao Tao estimates) in Ethiopian moist evergreen Afromontane forests: SMF: Small managed forests; LMF: Large managed forests; LNF: Large natural forests; and TOTAL: all sampled trees on which at least one orchid was found.

three forest types and had no indicator value. The dwarf orchid *Microcoelia globulosa* (Fig. D5), a species of forest margins and secondary growth, was a significant indicator for the SMF (indicator value IV = 38.5, p < 0.001). The strongest indicators for the LMF were *Diaphananthe tenuicalcar* (IV = 22.3; p < 0.001), a species of forest edges and wooded grassland, and *D. candida* (IV = 19.3; p = 0.002; Fig. D6). Several species of montane forest, secondary forest and open woodland were, also due to their high abundance, significant indicators for the LNF, with the highest indicator values for *Polystachya bennettiana* (IV = 65.2), *P. cultriformis* (IV = 43.5; Fig. D7) and *Bulbophyllum josephi* (IV = 42.2; Fig. D8) (all p < 0.001) (Appendix A).

The NMS ordination (final stress 26.69; 48.2% of variance explained) showed a clear separation of trees from the three forest types, with the main separation between natural and managed forests and a considerable overlap between LMF and SMF (Fig. 3). Mixed models with only Forest type as the independent variable showed highly significant effects of Forest type on all dependent variables (Appendix B). Pairwise comparisons showed that *S* was significantly higher in LNF compared to LMF, and significantly higher in LMF compared to SMF (Fig. 4a). N1 significantly decreased from LMF to SMF but was not different between LNF and LMF (Fig. 4b). Plot scores on NMS1 were significantly different between the three forest types, and plot scores on NMS2 were different between the three forest types.



NMS1: 31.1 % variance explained

Fig. 3. Community composition of epiphytic orchids (NMS ordination) on 279 sampled trees in moist evergreen Afromontane forest in southwestern Ethiopia. Trees are labeled according to three forest types: SMF: Small managed forests; LMF: Large managed forests; LNF: Large natural forests.

ent for LNF vs. LMF and SMF (Fig. 4c and d). The MRPP confirmed strong multivariate differences in species composition between forest types (T = -55.6), and forest types had a more homogenous species composition than could be expected by chance (A = 0.09, p < 0.001).

The reduced mixed models showed a consistent highly significant effect of the main effect Forest type on all species response variables (Table 2). Also tree dimension (either Tree height or Tree DBH, or both) consistently explained a large part of the variation between trees. Elevation of the tree (as a proxy of local climate) was never significant. Significant interactions between Tree type and Forest type, for *S* and *N*1, indicate that the effect of Forest type is different for late-successional compared to early-successional trees. Additional mixed models on a dataset with only the late-successional trees revealed that differences between the three forest types persisted, while they disappeared between LNF and LMF for the early-successional trees (results not shown). Pairwise comparisons (LSD) between forest types, based on the estimated marginal means from the reduced models (i.e. by keeping all other variables constant at their mean value), revealed that differences in S and N1 persisted between LMF and SMF, but that the difference in S disappeared between LNF and LMF. Marginal means of NMS1 scores remained significantly different between all forest types while tree scores on NMS2 remained significantly different for LNF vs. LMF and SMF (Appendix C).

4. Discussion

Our results first of all show a significant decrease in orchid species richness, and a change in community composition when coffee management intensifies from FC systems (LNF) to SFC systems (both LMF and SMF). These differences between the natural forest in the Gera area in the west, and both the small and large managed forests in the Jimma area in the east are unlikely to be related to climatic differences between the two regions which are situated at ca. 50 km from each other. First, these climatic differences are relatively minor, with an average year temperature and precipitation of 20.3 °C and 1777 mm, respectively, in the Jimma area; and 18.4 °C and 1783 mm in the Gera area. Second, tree elevation (as a proxy for microclimate) was not related to any indicator of orchid species occurrence in our mixed models. Although we were unable to find any historical data on epiphytic orchid occurrence in the

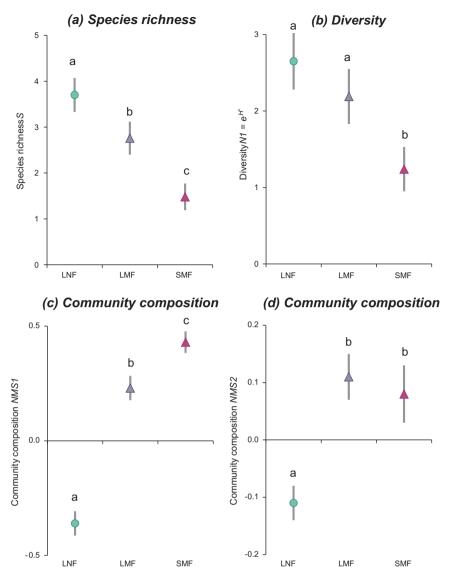


Fig. 4. Comparison of the average species richness/tree *S* (a), true diversity *N*1 (b) and community composition *NMS*1 and *NMS*2 (c and d) for epiphytic orchids in three forest types in Ethiopian moist evergreen Afromontane forests: SMF: Small managed forests; LMF: Large managed forests; LNF: Large natural forests. One standard error (+ and –) is indicated. Different letters denote statistically significant differences (LSDs) among the three forest types, according to a mixed model with forest fragment as the random factor and forest type as the fixed factor (see text for model details).

Jimma area that could support the idea of local species extinctions, we have no reason to assume a different original epiphytic orchid species composition, given the geological and climatologic similarity between the two regions.

The typical coffee management, aiming at increasing coffee shrub productivity through decreasing the canopy cover, results in a simplified forest structure, reflected by fewer and thinner stems, lower canopy height and reduced crown closure (Aerts et al., 2011; Senbeta and Denich, 2006). The number of stems (256/ha vs. 952/ha), canopy cover (56% vs. 82%) and the basal area $(21 \text{ m}^2/\text{ha vs. } 60 \text{ m}^2/\text{ha})$ are indeed significantly lower in the managed forests compared to the natural forests (Hundera et al., 2012). Interestingly, species richness differences between LNF and LMF disappeared when controlling for tree height and DBH, as shown by the pairwise comparisons of the marginal model means (Appendix C). This suggests that the mere removal of large trees from the managed forests is the main cause of epiphytic diversity decrease due to management intensification. Our data also showed that the smaller early-successional species C. macrostachys and M. ferruginea harbored a low epiphytic orchid richness while the larger late-successional *S. guineense* and *Sapium ellipticum* harbored a rather high richness in both the managed and natural forests.

Furthermore, changes in canopy structure due to large tree removal may also contribute to variation in microclimatic conditions, and increased impact of wind. Microclimatic variables, particularly solar radiation and air temperature, are indeed highly sensitive to changes in the overstorey canopy structure (Saunders et al., 1999) and may also contribute to the absence of many epiphytic orchid species from both managed forest types (Moorhead et al., 2010; Winkler et al., 2005). Epiphyte removal from trees and shrubs by farmers (personal observation; Fig. D9) may be an additional reason for the decline in species richness in the managed forests. Farmers consider them as parasites and believe that they have a negative impact on coffee production (Hylander and Nemomissa, 2008). Hietz (2005) and Moorhead et al. (2010) have reported the same practice in Mexico where coffee farms with epiphytes are perceived as unmanaged from a visual standpoint.

Even though a decrease in overall epiphyte diversity in anthropogenically disturbed habitats compared with primary forests has been reported before, for example in Central Mexico (Hietz, 2005;

Table 2

Results of the reduced mixed models relating Species richness (S), True diversity (N1), and the scores of the trees on the first and second NMS axes to the independent variables: successional stage of the tree (Tree type), tree height (Height), Tree diameter at breast height (DBH), Forest type (LNF, SMF or LMF) and elevation (m a.s.l.) of the tree.

Dependent variables	Effects	F	Р
S	Intercept	10.61	< 0.001
	Forest type	11.98	< 0.001
	DBH	20.35	< 0.001
	Height	17.56	< 0.001
	Tree type	2.80	0.10
	Forest type*Tree type	6.97	0.001
	DBH*H	9.91	0.001
N1	Intercept	4.95	0.02
	Forest type	8.81	< 0.001
	DBH	12.22	< 0.001
	Height	4.61	0.03
	Tree type	1.44	0.23
	Forest type*Tree type	3.44	0.033
	DBH*Tree type	6.82	0.009
NMS1	Intercept	15.66	< 0.001
	Forest type	42.40	< 0.001
	Height	7.73	0.006
	Tree type	6.49	0.011
NMS2	Intercept	5.67	0.018
	DBH	13.49	< 0.001
	Forest type	10.70	0.001
	Tree type	8.63	0.004

Solis-Montero et al., 2005), the Andes of Ecuador (Werner et al., 2005), and Venezuela (Barthlott et al., 2001), this is the first report on the impact of coffee management intensity on the species richness and community composition of epiphytic orchids in Afromontane forests. Also in SW Ethiopia, Hylander and Nemomissa (2008) studied the epiphyte diversity of solitary shade trees in even more intensively managed home gardens, and reported a decrease of vascular epiphytes compared to forest fragments of more than 10 ha. In an agroforestry context, a similar pattern of substantial decrease in epiphyte species richness was also reported for shaded cacao plantations in Ecuador (Haro-Carrión et al., 2009).

We also found significant differences between LMF and SMF with respect to S, N1 and community composition (NMS1). Interestingly, these differences between LMF and SMF persisted when comparing the marginal model means, i.e. when keeping Tree height and Tree DBH constant. As forest structure and canopy composition are not different between the LMF and SMF (Aerts et al., 2011), we believe that differences between these forest types are mainly related to their size differences, i.e. to forest fragmentation effects. Different mechanisms may explain these habitat fragmentation effects on the epiphytic orchid diversity and community composition of managed coffee forests. First, in small coffee forests, microclimate alterations may occur, as the whole of the forest fragment is affected by edge effects, through increased penetration of sunlight and wind, decreased humidity and increased temperature (Broadbent et al., 2008; Didham and Lawton, 1999). As the average distance to the forest edge of the trees sampled in SMF was only 22.7 m (as compared to 86.1 m in LMF), it is indeed likely that both orchid diversity and community composition were consistently altered by edge effect in the smallest forest fragments.

Next to modifying the habitat quality through edge effects, forest fragmentation may also have genetic consequences for the orchid populations. Reduced genetic variation and increased inbreeding within small and spatially isolated plant populations (Aguilar et al., 2008; Honnay and Jacquemyn, 2007) are commonly reported consequences of habitat fragmentation. Loss of genetic variation may result from the disruption of mutualistic interactions, since small fragmented plant populations may be less attractive to pollinators and thus more strongly pollen limited, leading to increased selfing and reduced reproductive success (Aguilar et al., 2006; Leimu et al., 2010). A recent population biological study on the epiphytic orchid *Myrmecophila christinae* (Parra-Tabla et al., 2011) indeed showed that habitat fragmentation resulted in decreased reproductive success and pollen limitation, and another study, on the coffee plant *Coffea arabica* in the same localities (Aerts et al., 2012), showed that forest coffee management resulted in cryptic genetic erosion.

5. Conclusion

Even though shade coffee cultivation is considered as a biodiversity-friendly practice (Moguel and Toledo, 1999; Philpott and Dietsch, 2003) and has been promoted as a conservation friendly development strategy (Conservation International, 2011), caution must be taken not to equate shade coffee cultivation to the benefit generated from the original forest what concerns biodiversity conservation (Tejeda-Cruz et al., 2010; Tscharntke et al., 2011). Agroforestry systems mimic natural forests and they can play an important role in biodiversity conservation in human-dominated landscapes (Bhagwat et al., 2008), including in the conservation of epiphytic orchids, but protection of pristine habitat remains essential (Anand et al., 2010; Tscharntke et al., 2011). Forest management to maximize coffee production by reducing structural complexity and tree composition as well as fragmentation through agricultural expansion and settlement has a detrimental effect on epiphytic orchids' diversity in Ethiopian coffee forests. Our results may also apply to other epiphytic species including ferns. Even though some endangered orchid species persist even in the smallest fragments, large managed forest fragments are better options for the conservation of epiphytic orchids than small managed forests. Ultimately, the preservation of the forest coffee system over large areas with little or no modification of the tree and shrub species composition and structure is crucial for the conservation of epiphytic orchids.

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Appendix A. Supplementary data

Data for this study are available at PANGAEA. http://dx.doi.org/ 10.1594/PANGAEA.788095. Supplementary data associated with this article can be found, in the online version, at http:// dx.doi.org/10.1016/j.biocon.2012.10.029.

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2012.10. 029. These data include Google maps of the most important areas described in this article.

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