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Effects of habitat fragmentation and coffee cultivation on the diversity of epiphytic orchids in Ethiopian Afromontane forests

by
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Dissertation presented in fulfillment of the requirements for the degree of Master in Biology

Academic year 2010-2011

ACKNOWLEDGEMENT

I started my education in Biology with a healthy interest in nature, environment and birds. Those boring plants, well, they would come with the job... Through my education my interest in plants got triggered and, more and more, they became a fascinating object to study. Orchids were an important part of this fascination and through Tine Meekers, I was able to make my first real scientific work around orchids. A year and half ago I first heard about the existence of this master thesis thanks to Olivier Honnay; travelling to a foreign country to study epiphytic orchids by climbing the trees. This combination of adventure, multicultural travelling, climbing, orchids and science seemed too good to be true...

A year ago, the VLIR UOS gave permission to sponsor the project and I was happy to book my flight. The preparation could begin! More than nine months ago I took my first steps on the great African continent. An eyeopener, an intercultural experience that never bored me a second! Five months ago I began writing this thesis and now finally I can write this part, as a final piece of my studies in Biology. Many thanks to everyone who helped me accomplishing this work:

- First of all I want to thank Prof. Olivier Honnay and Dr. Ir. Raf Aerts for their contributions. This work greatly benefited from their neverending advice, know-how, critics and corrections both in the field, while processing the results and on paper. I am also grateful to Philip Cribb and Kristoffer Hylander for advice and help with species identification.

- Special thanks to Koen Van Overtveld who came to Ethiopia to teach me how to climb trees (in a responsible way), but in the end taught me a lot more than that. Thanks for the training, the advice, the problemsolving, the interest, the stories, the chocolate, the friendship and so much more. Many thanks to the anonymous readers of this thesis for their useful suggestions.

- I want to thank Kitessa, Tijani, Abdu, Rashid, Aba'shiro and Sabit for their help with the fieldwork, their experience with Ethiopian forests and its inhabitants and for the pleasant environment they created to work in. It was a real pleasure working with you guys, betam ameseginalehu!

- Many thanks to the Ethiopian friends in Jimma; the drivers with their great skills, the guards with their great hugs, the students with their great interest and the university crew with their great Ungulal dabo. I want to thank Bestegaw Terefe in particular for the long and funny conversations. Again, ameseginalehu!

- Also, I'd like to thank the 'Faranji' in Jimma for their company. The dinners (from Kikil to fries), the discussions (from zebras to mosquitos), the travelling (from Seka to Bale), the experience (from Yonas hotel and breweries to hippo-hunt and hyena encounters),... We shared quite the adventure there. Special thanks to Inez for her great share in the fieldwork, the large amount of patience and her sense of humour.

- Last but not least I want to thank my parents, for all the obvious but especially for that what is not obvious. Thanks for the trust and patience, not only this year but all the years before.

ABSTRACT

Question: What is the effect of habitat fragmentation and coffee cultivation on the diversity of epiphytic orchids in montane rainforest? If a shift in species composition or loss in diversity occurs, can this be explained by environmental variables?

Location: Jimma zone, Ethiopia. Semi-plantation coffee production system in forest fragments near Garuke, (7°44’N, 36°44’E), a semi-forest coffee production system called Fetche (7°42'N, 36°46'E) and two large, natural sites of wild coffee forests, belonging to the Belete-Gera National Forest Priority Area (Qacho 7°46'N, 36°17'E and Afalo 7°38’N, 36°13'E).

Methods: Epiphytic orchids and environmental variables were assessed in 339 10×10 m^2 plots. Every plot consisted of two subplots, the shrub layer and the tree layer. Trees were climbed to measure orchid abundance and richness. The sampled plots were located in different small and isolated fragments in Garuke (151 plots), in Fetche (49) and in Gera (139). The plots of Fetche were added to those of Garuke to analyse data between two forest types; plots in fragmented forests (200) vs. plots in continuous forests (139). Diversity indices were calculated and plots were analysed with NMS and ISA and related to environmental variables. Spearman rank correlations were used for the continuous variables and Mann-Whitney U tests for discrete variables.

Results: The species community of the fragmented forests differed from that of the continuous forests. For both the tree and the shrub layer a different species composition occured between the forest types. For both layers, the fragmented forest had a lower diversity in epiphytic orchids. Community differences were related to forest type, the size of the sampled tree and the distance of the plot to the forest edge. When plots of fragmented forests were analysed seperately, community differences were mostly related to fragment size and distance to the forest edge. In fragmented forests compared to continuous forests, a higher orchid abundance was found in the shrub layer and orchids did occur lower in the tree. Also, orchid richness in the host tree was correlated with tree species.

Conclusions: The epiphytic orchid communities change and the diversity declines when the forest becomes more fragmented and cultivated. As a respons to disturbance, a downward shift is found in the vertical distribution of orchids, and certain host tree species are more valuable in conservation of orchids than others. Epiphytic orchids are useful indicators of forest disturbance, emphasising the importance of epiphytic orchids for conservation projects. Protected areas of undisturbed forest will be necessary to assure the conservation of epiphytic orchid diversity in Ethiopia.

Keywords: Epiphytes – Orchidaceae – Afromontane forest - Ethiopia - Habitat fragmentation – Forest cultivation – NMDS

SAMENVATTING

Onderzoeksvraag: Wat is het effect van habitatfragmentatie en koffieteelt op de diversiteit van epifytische orchideeën in montaan regenwoud? Als er een verschil of verlies in soorten wordt gevonden, kan dit dan verklaard worden door omgevingsvariabelen?

Locatie: Jimma zone, Ethiopië. Semiplantage koffie productiesystemen in bosfragmenten in Garuke (7°44’ N, 36°44’ E), een semibos koffie productiesysteem genaamd Fetche (7°42' N, 36°46' E) en twee grote, natuurlijke bosfragmenten, beschouwd als wild koffiebos, behorend tot het Belete-Gera National Forest Priority Area (Qacho 7°46' N, 36°17' E en Afalo 7°38’ N, 36°13' E).

Methode: Epifytische orchideeën en omgevingsvariabelen werden opgemeten in 339 10×10 m^2 plots. Elk plot bestond uit twee subplots, één waar de struiklaag en één waar de boomlaag werd onderzocht. Bomen werden beklommen om de rijkdom en abundantie aan orchideeën op te meten. De gesamplede plots bevonden zich in verschillende kleine en geïsoleerde fragmenten in Garuke (151 plots), in Fetche (49) en in Gera (139). De plots van Fetche werden aan die van Garuke toegevoegd om een analyse te kunnen maken tussen twee bostypes; plots in gefragmenteerd bos (200) vs. plots in continue bos (139). Diversiteitindices werden berekend en plots werden geanalyseerd met NMS en ISA en gecorreleerd met omgevingsvariabelen. Spearman rank correlaties werden gebruikt voor continue variabelen en Mann-Whitney U tests voor discrete variabelen.

Resultaten: De soortsgemeenschappen van het gefragmenteerd bos verschilden van die van het continue bos. Zowel voor de struik- als voor de boomlaag werd een verschillende soortensamenstelling gevonden tussen de bostypes. De diversiteit aan epifytische orchideeën was lager in het gefragmenteerd bos en dit zowel in de struik- als in de boomlaag. Verschillen in gemeenschappen waren vooral gerelateerd aan een verschil in bostype maar ook aan de grootte van de gesamplede boom en de afstand van de plot tot de bosrand. Wanneer de plots van het gefragmenteerd bos apart werden geanalyseerd, dan waren verschillen in gemeenschappen vooral gerelateerd aan de oppervlakte van het fragment en de afstand tot de bosrand. In gefragmenteerd bos werd, relatief ten opzichte van continue bos, een hogere abundantie aan orchideeën gevonden in de struiklaag en in de bomen kwamen de orchideeën lager voor. Ook bleek de soortenrijkdom aan orchideeën in de boom gecorreleerd met de boomsoort.

Conclusie: De epifytische orchideeëngemeenschap verandert en de diversiteit daalt, naarmate het bos meer gefragmenteerd en gecultiveerd geraakt. Wanneer verstoring toeneemt vinden we een stijging van het aantal orchideeën in de struiklaag en een hoger percentage aan orchideeën in de lagere boomzones. Sommige boomsoorten blijken waardevoller in het behoud van orchideeënrijkdom dan andere. Epifytische orchideeën zijn bruikbare indicatoren van bosverstoring wat het belang benadrukt van epifytische orchideeën voor conservatiedoeleinden. Het is belangrijk om reservaten aan te leggen van onverstoord bos voor de conservatie van de diversiteit aan epifytische orchideeën in Ethiopië.

Sleutelwoorden: Epifyten - Orchidaceae – Afromontaan bos – Ethiopië - Habitat fragmentatie – Bosmanagement – NMDS

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1. INTRODUCTION

"The forest is a peculiar organism of unlimited kindness and benevolence that makes no demands for its sustenance. It extends generously the products of its life activity. And it affords protection to all beings, offering shade even to the axe-man who destroys it" (Gautam Buddha)

1.1. Epiphytic orchids

1.1.1. Epiphytes

Epiphytes are plants that use other plants as a habitat (Fig. 1). They are not considered parasites because they do not derive any kind of nutrition from their host plant. They derive water and nutrients both from the air and rain, and from the dead bark and debris, accumulating around the epiphyte. Epiphytes are mostly found in the tropics and subtropics but especially mosses, liverworts and lichens can occur as epiphytes in almost every environment with trees. Epiphytes are photosynthetic and thus capable of producing their own energy. They use the plants they grow on only for physical support (Hanski & Gilpin 1997). The big advantage for epiphytes, besides the avoidance of competition with other plants, is the benefit of growing higher in the trees and as such receiving more light than terrestrial plants at the same location (Benzing 2004).

Fig. 1: Ferns, orchids, bryophytes and lichens growing as epiphytes on a tree in the Belete-Gera National Forest Priority Area.

Because epiphytes occupy this special habitat, they are in general more dependent on the environmental conditions than terrestrial plants. The adaptation to life above the soil makes them more sensitive to environmental changes (Engwald *et al.* 2000; Padmawathe *et al.* 2004). In vascular epiphytes, the colonization and establishment of new seedlings is a rather slow process, making them more vulnerable for rapid environmental changes. They experience tree crowns as a mosaic of suitable and unsuitable habitats, where suitable habitats are species specific and, sometimes, only present in small and discrete patches (Hanski & Gilpin 1997).

Epiphytes are seen as an important component of biodiversity in tropical forest ecosystems. They can be very abundant in tropical forest canopies and can account for up to half of forest-plant richness (Benzing 1990; Engwald *et al.* 2000; Nieder *et al.* 2001). Besides their obvious biodiversity aspect, epiphytes have an important ecological function. They are part of ecosystem processes and have functions in nutrient and water cycling. Specifically in tropical forest ecosystem, a change in epiphyte composition can have cascading effects, affecting ecosystem services in general (Moorhead *et al.* 2009).

Epiphytes can be used as indicators of forest disturbance but they also provide resources and niche possibilities for canopy-dependent fauna (Benzing 1990; Cruz-Angon & Greenberg 2005). Since they are useful climatic indicators (Richter 1991), they can be used as a warning system for changing conditions in microclimate (Haro-Carrión *et al.* 2009) and even as indicators of global climatic change (Benzing 1998).

1.1.2. Epiphytic orchids

The Orchidaceae is currently believed to be the second largest family of flowering plants in the world with more than 22,000 species described. Although the family originated from terrestrial orchids, most of the species are epiphytic which can only be found in the tropics and subtropics (Benzing 2004). Epiphytes account for c. 70% of all the orchid species (Stevens 2001). Epiphytic orchids have no vascular connection with their host but the roots make sure the orchid is anchored to the host. The roots also function as nutrient and water storage and uptake mechanism. Cells in the roots contain chloroplasts for active photosynthesis. Some orchids have no leaves and fully depend on their roots for energy (Fig. 2).

Fig. 2: *Microcoelia globulosa*, a leafless orchid, growing on a coffee shrub. Picture is rotated 90°.

Since they cannot rely on a regular supply of water via the soil, epiphytic orchids have some xerophytic adaptations. Their leaves are rather leathery, often being very succulent. The leaves have a thick cuticula that reduces water loss (Stevens 2001; Benzing 2004). A velamen develops in the roots (Fig. 3A). This is a tissue supporting one or more layers of dead cells. Special thickenings in the cell wall prevent the collapse of the cells and provide some protection for the roots against mechanical injury. Cells in the velamen can rapidly absorb water in wet conditions, even passively from the atmosphere (Benzing 2004). But in dry conditions, the cells only contain air and act as a barrier to prevent water loss via transpiration from the water conducting tissues in the inner part of the roots. The velamen reaches its maximum development in the roots that hang free in the air (Oliveira & Sajo 1999). Most epiphytic orchid species form enlarged stem segments called pseudobulbs, from which the leaf grows (Fig. 3B). Being succulent, these pseudobulbs can store nutrients and water. The pseudobulbs swell or shrink, depending on the external moisture conditions. To minimize water loss, epiphytic orchids make use of the crassulacean acid metabolism (CAM), allowing for the uptake of CO_2 during the night (Motomura *et al.* 2008). These adaptations are necessary for epiphytic orchids to overcome seasonal rainfall patterns, which sometimes results in months with alsmost no precipitation (Benzing 2004).

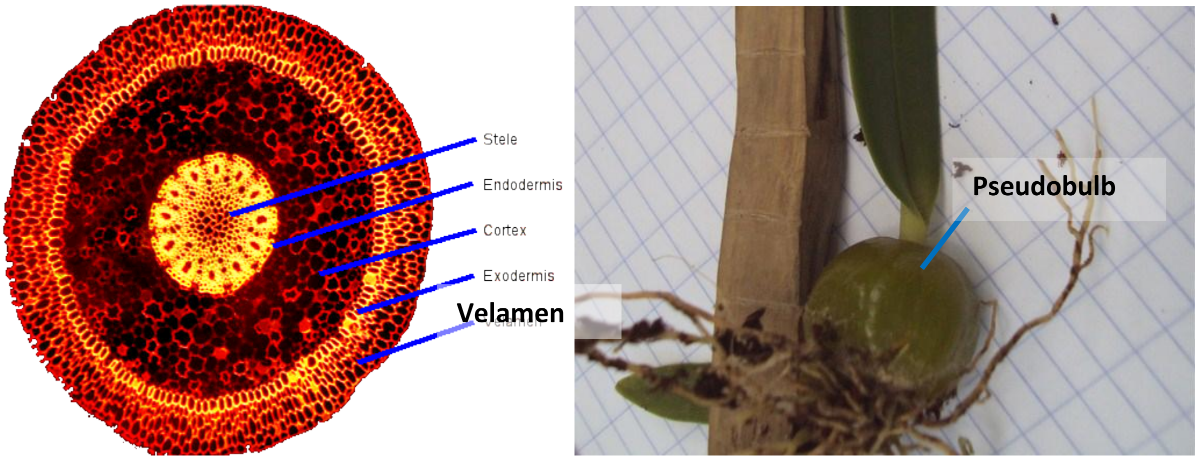

Fig. 3A: Cross section of an orchid root with indication of the velamen (Barkalow n.d.). **B:** Pseudobulb of a *Bulbophyllum* species.

The distribution of epiphytic orchids in the forest is a subject which is rarely studied. Most orchid species occur clumped in a tree around the orchid mother plant. Orchids were shown to cluster more strongly than any other group of epiphytes (Hietz & Hietz-Seifert 1995). The reason for this phenomenon is that growing close to conspecific plants, chances are higher to form an association with mycorrhiza (Hietz & Hietz-Seifert 1995; Diez 2007). The seeds of epiphytic orchids are generally almost microscopic and are mainly dispersed by the wind. Orchids need microsites with specific levels of humidity, temperature and suitable substrate that fit their ecological requirements for germination and establishment (Winkler *et al.* 2005). Orchid seeds are very numerous because chances to be dropped at the right microsite are small and a beneficial association with mycorrhiza is often necessary for germination (Winkler *et al.* 2009). Host tree species seems to be an important aspect of epiphytic orchid diversity (Haro-Carrión *et al.* 2009). The roughness of the bark, the water holding capacity of the bark and bark pH are important characteristics influencing epiphyte diversity (Patino & Gonzalez 2011). The establishment of orchid seeds and seedlings can be increased by a more corrugated bark or larger branches. Also, the presence of other epiphytes, especially bryophytes, can facilitate the establishment (Hietz *et al.* 2002). The extent of dispersal limitation acting on epiphytic orchids in fragmented forests remains largely unstudied (Wolf 2005).

1.1.3. Ecological importance

Epiphytes in general are an important part of the biodiversity in the rainforests and can contribute even more to the diversity by offering food and habitat to other species. Orchids in general are a broad and diverse group with many species, sensitive to ecosystem or environmental changes. The same is true for epiphytic orchids. However, not every species is affected in the same manner by human disturbance. Some orchid species are indicated to grow even better in more disturbed habitats (Solis-Montero *et al.* 2005; Werner *et al.* 2005;

Hietz *et al.* 2006). Because of their vulnerable lifestyle and the broad differences between species, epiphytic orchids can be used as indicators of forest quality.

Orchid species do not grow random in the tree. The species composition shows a vertical stratification where different species occur in different layers in the canopy of the tree, depending on their microclimatic needs. Engwald *et al.* (2000) indicated that epiphytes of montane rainforests in particular are more vulnerable, compared to other forests, to changes in their environment. This is probably due to the importance of slowly growing, structural old trees in montane rainforests. Changes in the vertical distribution of the epiphyte species due to changes in microclimatic conditions can be used to indicate human disturbance (Padmawathe *et al.* 2004; Haro-Carrión *et al.* 2009). Identifying the species that are more sensitive to changes and those that are able to flourish in disturbed habitats can help to indicate forest disturbance.

Orchids in general and epiphytic orchids in specific are often used for conservation measures. Because of their spectacular flowers or because they are often rare or endemic, orchids can be used as flagship species for (sub)tropical forests. This helps to raise funding for research and conservation efforts, to gain the attention of the public and to enhance ecotourism. They can be of great importance for plant conservation and to protect certain orchid rich habitats, as such protecting whole ecosystems (Demissew *et al.* 2004).

1.2. Effects of forest fragmentation and management on epiphytic orchids

1.2.1. Forest fragmentation

Habitat fragmentation is considered as one of the three main causes behind the present biodiversity crisis (Young & Clarke 2000). Tropical forests are under considerably high human threat. Habitat fragmentation affects the ecology of tropical forests in many ways, and it consists of three major components: the direct loss of habitat, a reduction in the size of the remnant fragment and an increased isolation of the fragments (Andren 1994).

When large tracts of forests are dissected, organisms are exposed to different biotic and abiotic changes. Fragmentation changes the quality of the forest by altering its climatology (e.g. wind velocity and humidity), forcing species to cope with changes in microclimate and ecological functions. It also increases the amount of edge habitat with diverse ecological consequences. Epiphytes are believed to have great potential as indicators of forest edge effects (Esseen & Renhorn 1998).

Fragmentation usually reduces population size, making species more vulnerable to extinction due to stochasticity and the possible loss of genetic variation. Less specialized pollinators can be expected in small and isolated habitats (Roubik 2002; Honnay *et al.* 2005). This can reduce reproductive success of plants. Individuals from larger populations usually have higher fruit success than individuals from smaller ones (Leimu & Syrjanen 2002; Tremblay *et al.* 2005). The potential for a species to adapt to changes, whether environmental or climatic, decreases when its genetic diversity is reduced (Young & Clarke 2000). However, some tropical plants (e.g. some epiphytic orchids) occur naturally at low densities in tropical forests. These species can have certain aspects in their life history that maintain or even augment reproductive success after fragmentation took place. This can occur through long distance pollination (Murren 2002). This suggests that the effect of fragmentation is species-specific.

Fragmentation can affect the distribution and diversity of epiphytic orchids. Different aspects of the life history of epiphytic orchids suggest increased extinction risk when populations become fragmented. Because tropical orchids are often dependent on one or few specialized pollinators for successful fruit set (Ackerman 1996), it can be expected that they suffer from pollinator limitation in small fragments with small populations. The general lifestyle of epiphytic orchids also makes them more vulnerable to changes in climatologic conditions, especially decreased air humidity and precipitation (Murren 2002). These aspects put epiphytic orchids at an increased risk of local extinction after forest fragmentation.

1.2.2. Management changes

Conversion of tropical primary forest into anthropogenic habitats has consequences for the biodiversity of the forest. Epiphytes are one of the first life forms to be affected by changes in primary forests because they occupy forest canopies (Sodhi *et al.* 2008). When epiphyte diversity is compared between natural forests and anthropogenic habitats, most of the secondary habitats show a reduced diversity (Barthlott *et al.* 2001; Werner *et al.* 2005), though the extent of the changes in diversity can vary between study sites and habitats.

A number of studies have been investigating the human impact on epiphyte diversity and some of them do consider the habitat conversion to secondary forest types. Few studies were restricted to single taxa such as bromeliads and/or orchids (Hietz *et al.* 2006). In general, changes in microclimatic conditions because of the selective logging of certain tree species, can strongly decrease epiphyte richness (Hietz-Seifert *et al.* 1996; Barthlott *et al.* 2001; Werner *et al.* 2005). Haro-Carrión *et al.* (2009) studied the contribution of shade cacao plantations to vascular epiphyte conservation and showed a reduced diversity of epiphytes in plantations relative to natural forest. But no difference was found in species richness of Orchidaceae.

Köster *et al.* (2009) showed a loss of epiphyte species in secondary forest with young secondary forests being less diverse than older secondary forests. Interestingly, this study showed no significant effect of spatial parameters such as fragment area, distance to edge or distance to primary forest on epiphyte diversity.

Barthlott *et al.* (2001) compared secondary vegetations with primary montane rainforest in the Andes. The study found a lower diversity of epiphytes in general and Orchidaceae in specific, for the secondary vegetation. This was not the case in a study of Moorhead *et al.* (2009). They found the orchid composition to be equally rich in polyculture coffee farms and in natural forests. However, when polyculture farms and natural forests were compared with monoculture coffee farms, a difference in richness was found. Other studies show that epiphyte diversity and abundance is lower in shaded coffee farms (Mexico) and home gardens (Ethiopia) than in nearby natural forests (Hietz 2005; Hylander & Nemomissa 2008). Some studies show that epiphyte diversity is positively correlated with increasing tree size (Hietz 2005; Moorhead *et al.* 2009).

Hietz *et al.* (2006) studied the abundance of epiphytic orchids and bromeliads in a montane forest in Mexico. They concluded that disturbance does have complex species-specific effects, depending on many factors like host tree species. Thus it seems clear that not every orchid species reacts alike; drought-resistant species may benefit from the disturbance resulting in an increased occurrence in managed ecosystems (Larrea & Werner 2010). Especially species that require more shade and/or high humidity will decline or go extinct due to fragmentation and increased forest management (Hietz 2005; Werner *et al.* 2005; Wolf 2005). How much these species are negatively affected mainly depends on the degree of disturbance, the age of the secondary forest and the size and species composition of the remnant trees (Padmawathe *et al.* 2004). How epiphytes on the remaining trees react or how colonization on younger trees occurs, remains more elusive. Haro-Carrión *et al.* (2009) studied the vertical distributions of vascular epiphytes in shade cacao plantations relative to natural forest. They observed a downward shift of epiphytes on the remnant trees in shade cacao plantations.

Solis-Montero *et al.* (2005) studied the population structure of certain epiphytic orchid species in a shade-coffee plantation in Mexico. They concluded that it is possible for orchid species to survive and reproduce in coffee plantations when the right microclimate conditions are present. Although plantations are not able to replace the original conditions of the primary forest.

To summarize, results of previous studies confirm that the composition and diversity as well as the vertical distribution of epiphytes can be used as an indicator of human-induced disturbance in a forest landscape (Hietz *et al.* 2006; Hylander & Nemomissa 2008; Haro-Carrión *et al.* 2009). To minimize the loss in epiphyte biodiversity, the maintenance of large, forest-like trees in managed plantations could help to conserve epiphyte diversity, not only in the canopy but also in the understorey (Haro-Carrión *et al.* 2009). The crop itself can also contribute to the overall species richness. It can increase the habitat area for epiphytes and improve the microclimatic conditions (Hylander & Nemomissa 2008).

1.3. Epiphytic orchids in the coffee forests of Southwest Ethiopia

The forested area in Southwest Ethiopia is under considerably high human threat. There are some major driving forces that increase pressure on the coffee forest in SW-Ethiopia. The most important is the rising population pressure causing deforestation for new settlements and agricultural land, as well as general overexploitation of the remaining forest. The others are road construction, making the forests more accessible, a poor policy and legislation with almost no control on illegal deforestation and the rising demand for coffee worldwide (Gove *et al.* 2008; ICO 2011).

Wild coffee, *Coffea arabica* L., is native to Ethiopia and grows as an understorey shrub species in Afromontane rainforests between 1000 and 2000m above sea level (asl) (Vavilov 1951). The local communities in Ethiopia have developed a long tradition of managing the forest for coffee production which is nowadays the main export product of Ethiopia (FAO & WFP 2009). This traditional management has only minor effects on the structure and biodiversity of the forest. Even today an important part of Ethiopian coffee beans (c. 35%) is produced in traditional coffee production forests. But with the rising demand for coffee, and its higher prices (ICO 2011), the management intensifies, aiming for higher yields (Aerts *et al.* 2011).

Coffee yields are much higher in semi-plantation coffee systems (SPC) and semi-forest coffee systems (SFC) than in forest coffee systems (FC) because of forest management (Schmitt *et al.* 2009). Therefore, in forests in SW Ethiopia that are cultivated for coffee, the undergrowth is removed at least once a year to avoid competition with non-coffee shrubs. New coffee seedlings are planted whereas older shrubs are pruned to increase growth efficiency (Aerts *et al.* 2011). The tree layer is managed as well: both tree species that are less efficient in shading and slow growing species are cut, resulting in 30 % less canopy trees in SFC (Schmitt *et al.* 2009). Even the trees that are used as shade trees are managed, often for wood extraction. These modifications to the forest have led to a uniform, species poor tree canopy and a single-species (coffee-)shrub layer (Fig. 4) (Schmitt *et al.* 2009; Aerts *et al.* 2011). In more intensely managed coffee forests, there is no intermediate layer anymore. In the long term this will have serious implications for the regeneration of the forest when the mature trees reach a post-productive stadium (Aerts *et al.* 2011).

Fig. 4: Semi-plantation coffee system with an open, species poor canopy and a uniform coffee shrub layer. Picture is taken from the tree at approximatly 6 m above the ground.

Some of the forest relicts, for example on more steep slopes, have been conversed to coffee forests. These relicts, which can vary greatly in size, are situated in an agricultural landscape matrix (Fig. 5). Depending on the quality of the surrounding matrix, it can be expected that these processes of fragmentation and intensified management have caused significant changes in abundance and diversity of forest plant species. Comparisons of epiphytes in forests and coffee agroecosystems show that forests in SW Ethiopia generally maintain higher richness and abundance than coffee agroecosystems (Hylander & Nemomissa 2008, 2009).

Fig. 5: Forest fragments in a matrix of maize fields, home gardens and grazing land.

Orchidaceae is, with around 167 species in 37 genera, the fifth largest family in the Flora of Ethiopia and Eritrea. Around 15% of the orchids in Ethiopia are endemic with 22 species being terrestrial and only six species being epiphytic. The orchid flora shows a decline in species richness from the southwest to the northeast, quite similar to the decreasing rainfall patterns (Demissew *et al*. 2004). Only 16% of the orchids are epiphytic or lithophytic (growing on rocks). Of them, the majority can be found in the more forested areas of west and SW Ethiopia. Epiphytic orchids in this more remote part of Ethiopia are poorly represented in reference collections and little is known about their distribution, physiology, ecology and conservation status. For a lot of epiphytic orchids, Ethiopia is the northern-most extent of the range of the species. This can in part explain why the share of epiphytic orchids in the total Ethiopian orchid family is rather low (worldwide around 70% of the Orchidaceae are epiphytic). It is suspected that many epiphytic orchids are threatened in Ethiopia because of massive deforestation. Although the conservation status for a lot of epiphytic orchid species in Ethiopia is not known, many species appear to be rare and/or endangered (Demissew *et al*. 2004).

Polystachya is the genus that is best represented in the list of epiphytic orchids in Ethiopia. It is a pantropical genus with its diversity centre in tropical Africa. Twelve species are found, mostly in more wet forested areas although some can survive dry conditions by losing their leaves in the dry season. Some of the species in this genus, e.g. *P. cultriformis* (Fig. 6A), are widespread and common in tropical Africa whereas others, e.g. *P. caduca* (Fig. 6B), are endemic for Ethiopia (Demissew *et al.* 2004).

Fig. 6A: *Polystachya cultriformis*. **B:** *Polystachya caduca.*

1.4. Problem statement and objectives

Changes in richness and abundance of different taxa have often been attributed to responses to disturbances. Deforestation in combination with changes in forest management has caused great changes in the pristine forest landscape of SW Ethiopia, leading to significant effects on the biodiversity of the area. Many studies have been studying the effect of human disturbance on biodiversity in different kind of landscapes. In the past, most studies focused on terrestrial plants for their research because they are easier to sample and the metapopulation structure is better known (Avila-Diaz & Oyama 2007). Currently, the focus lies on studying the epiphyte biodiversity in general because epiphytes are more sensitive to changes (Padmawathe *et al.*2004; Hietz 2005; Köster *et al.* 2009).

Previous studies have shown the negative effect of forest fragmentation and human disturbance on the diversity of epiphytes. This research has focused on an important group of epiphytes to investigate the effect on the composition and diversity of epiphytic orchids in the cultivated coffee forests around Jimma, Ethiopia. We aim to compare the orchid species diversity in semi-coffee plantations, semi-forest coffee systems and more natural coffee forest. In general, we expect the diversity and abundance of orchids to be lower in the cultivated and fragmented forest plots.

The study has the following objectives:

1. Identify a change and/or loss in diversity and communities of epiphytic orchid species between more pristine, continuous forest and fragmented coffee forest.
2. Establish a relationship between environmental variables and epiphytic orchid diversity.
3. Investigate if epiphytic orchids show vertical migration with increasing disturbance in the upper canopy.
4. Identify a relationship between orchid richness and host tree species.

2. MATERIALS AND METHODS

2.1. Study area

The study area consisted of three sites within 70 km west-northwest of Jimma. Jimma is a city situated in the Oromiya region in the highlands of Southwest Ethiopia (Fig. 7). The Oromiya regional state is the biggest of the nine federal states of Ethiopia. The forest index in the southwestern part of the country is 18%, accounting for more than half of the remaining forest area in the entire country; forests account for less than 3% of the surface of Ethiopia (Gole 2003).

The study area is situated between 1800 and 2100m asl. There is a humid, subtropical climate, with a yearly rainfall of about 1500mm or more, a short dry season and relatively high cloud cover. A peak in rainfall occurs between July and September (long rainy season) and a smaller peak occurs between March and April (short rainy season). Differences in temperature throughout the year are small with a mean minimum and maximum annual temperature of 11.9 and 26.4°C (Schmitt, 2006).

Species composition and altitude suggest that the forest in the study area is probably best classified as Afromontane rainforest (Van Mechelen 2009; Aerts *et al.* 2011). This forest occurs in the southwestern part of Ethiopia with an annual rainfall between 750 and 1500mm (Friis, 1992). This forest occurs in Ethiopia only in the highlands (elevation between 1500 and 2600m). The canopy in the drier part of the rainforest is dominated by *Afrocarpus falcatus* but as rainfall increases, *Pouteria adolfi-friederici* becomes more prominent (Demissew *et al.* 2004). The latter was the dominant tree in the continuous forest where we have done part of the sampling. Below these emergent trees (>25-30m) an almost continuous canopy exists of medium-sized trees with species such as *Ilex mitis*, *Prunus africana*, *Albizia* sp. and *Olea* sp., *Polyscias fulva*, *Sapium ellipticum* and *Syzigium guineese* subsp. *afromontanum* (For a full list of sampled tree species, see Appendix B). Lianas and epiphytes are widespread in the trees and understorey of the forest (Demissew *et al.* 2004). In canopy gaps, the ground cover is rich in grasses and herb species (Gole *et al.* 2003).

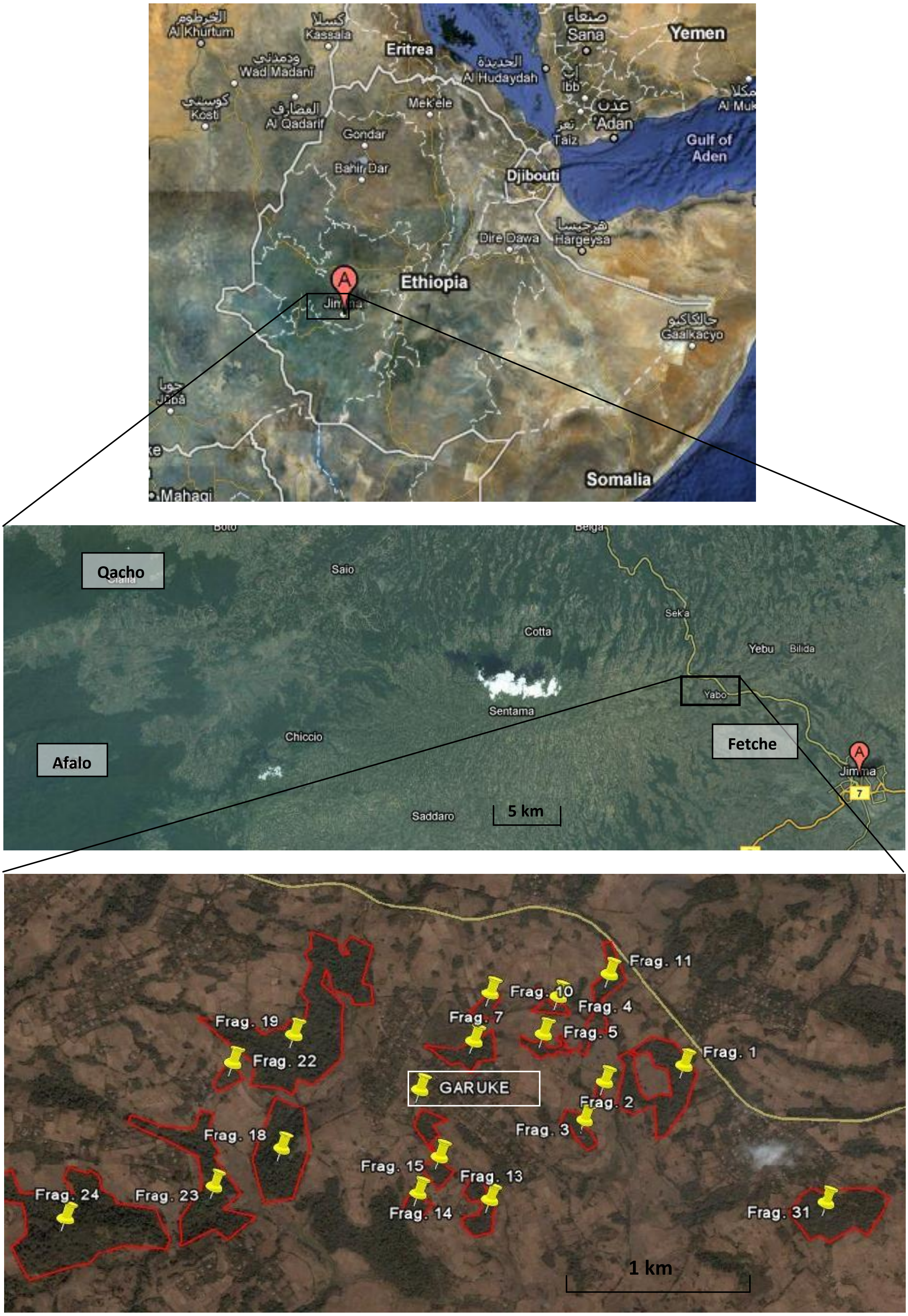

Fig. 7: Location of sampled plots in selected fragments in Garuke (Under), Jimma zone (Middle), Ethiopia (Upper). Satellite imagery©2009 DigitalGlobe, Google Earth.

2.1.1. Study sites

Garuke: The site of Garuke is located c. 10km northwest of Jimma. The site is named after the village of Garuke (7°44’ N, 36°44’ E; elevation 2000–2100m) and can be reached on an asphalt road by car or public transport within 20 minutes from the city of Jimma. The landscape is heavily fragmented and there is a high degree of human disturbance. In this area, forest fragments of different size and management intensity lie within a matrix of grazing land, Eucalypt plantations, small villages or settlements and crop fields, mainly with Maize and Teff (Aerts *et al.* 2011).

The forest fragments here have been cultivated for quite some time by farmers as coffee plantations. Fragments are owned by different coffee farmers. Each owner works with a different management intensity in both the tree layer and the shrub layer. Management in the tree layer consists of thinning the canopy to create optimal shading conditions for the coffee shrubs. Managing the shrub layer is done by the removal of competing shrubs (Fig. 8A) and old or unproductive coffee. Moreover, planting of new coffee seedlings and pruning of older coffee shrubs (Fig. 8B) for higher productivity are common practice (Aerts *et al.* 2011). Thinning of the canopy has resulted in the disappearance of almost all emergent trees (e.g. the climax species *Pouteria adolfi-friederici*) because the shade of these species is too deep for maximum coffee growth, and because the wood is of high economic value (Gole *et al.* 2003). The trees that currently dominate in this forest type are pioneer or secondary species such as *Albizia gummifera*, which are typical for secondary or disturbed forest because they have a relative high growth rate in gaps, created by coffee management (Chapman *et al.* 2002). The average size of forest fragments in this region is 4 ha (Van Mechelen 2009). We sampled 18 fragments in Garuke (Fig. 7), ranging in size from 0.25 ha up to 24 ha. The forest fragments in Garuke are considered semi-plantation coffee production systems (SPC).

Fig. 8A: Active removal of shrubs, other than coffee, in cultivated forests. **B:** Older coffee shrubs are pruned for higher productivity.

Fetche: The site of Fetche (7°42' N, 36°46' E) is situated less than 10km west-northwest from Jimma but is further from the asphalt road than the Garuke site. The remnant forest here is less fragmented resulting in 1 large cultivated “fragment” of approximately 100 ha surrounded by agricultural landscape. In this fragment we sampled 49 plots. Due to the proximity of Jimma city, this forest is of high interest for the production of coffee beans. Since the forest fragment has many different owners, the management intensity varies from very intensive to intermediate. Besides disturbance due to coffee productivity, the forest is also used for other functions such as firewood collection and charcoal production. The Fetche forest is considered to be a semi-forest coffee production system (SFC).

Gera: The third site we sampled is situated in the Gera sector of the Belete-Gera National Forest Priority Area; a large area of continuous forest with less disturbance and management than the previous sites. This site is situated c. 60km west of Jimma. The road between Jimma and the site is only partially surfaced with asphalt. We visited two areas within this site: Afalo and Qacho. Due to recent deforestation, Qacho (7°46' N, 36°17' E) is no longer connected to the larger forest complex of the Belete-Gera forest. In Qacho, wild coffee beans are collected and big trees are removed for construction and firewood, especially at the forest edge. At some sites in the forest, the canopy is partially removed and young shrubs were planted (Fig. 9). Deeper in the forest, the wild coffee shrubs grow almost unmanaged in what can be classified as a less disturbed Afro-montane rainforest. Around the small village of Afalo (7°38’ N, 36°13' E) the tree layer was less disturbed, but the shrub layer was often managed with clearance of non-coffee shrubs and even sowing of coffee seedlings. The forest in Qacho and Afalo is considered to be wild coffee forest (FC systems).

Fig. 9: Forest disturbance in the continuous forest. Clearance of shrub layer, canopy thinning and plantation of young coffee shrubs in Gera.

2.1.2. Sampling sites

In our study area, we selected forest fragments of different size and different level of management intensity in Garuke and Fetche, and we also sampled the large continuous forest in Gera. Within each forest fragment we sampled a number of plots, depending on the size of the fragment. These plots consisted of one mature tree in the centre of a ground surface plot of 10m·10m. In smaller fragments we sampled less plots than in larger fragments (Table 1). We used a random design and a density of approximately one plot per 0.5 to 1.5 ha. Within forest fragments, sample plots were located >25m apart to guarantee sample independence. Not every fragment was sampled equally because of sampling difficulties related to heavy rainfall, safety conditions or extremely time consuming plots. Nevertheless, a clear positive relation (R^2=0.714) remains between the sample size and the size of the fragment. In total, 339 plots were sampled over the three sites. All plots are situated between 1800 and 2100m asl. In Garuke, we sampled 151 plots, in Fetche 49 and in Gera forest 139 plots. The sampling was executed over a period from mid August till mid November 2010 (12/08/2010 – 11/11/2010) with 34 days of active sampling.

Table 1. Sampled fragments. Region: Garuke (GA), Fetche (F), Gera (G)

Fragment	Region	Surface (ha)	Management	n° of sampled trees	GPS coordinates
1	GA	8	SPC	15	7°43'59" N, 36°45'4" E
2	GA	0.25	SPC	3	7°43'56" N, 36°44'50" E
3	GA	1.86	SPC	5	7°43'49" N, 36°44'47" E
4	GA	1.1	SPC	3	7°44'12" N, 36°44'42" E
5	GA	1.8	SPC	7	7°44'5" N, 36°44'40" E
7	GA	4	SPC	11	7°44'4" N, 36°44'28" E
10	GA	1.5	SPC	7	7°44'12" N, 36°44'31" E
11	GA	3.7	SPC	6	7°44'16" N, 36°44'51" E
13	GA	3	SPC	7	7°43'35" N, 36°44'30" E
14	GA	1.24	SPC	3	7°43'36" N, 36°44'18" E
15	GA	2	SPC	9	7°43'43" N, 36°44'21" E
18	GA	10	SPC	10	7°43'44" N, 36°43'54" E
19	GA	24	SPC	21	7°44'5" N, 36°43'57" E
22	GA	1	SPC	4	7°44' N, 36°43'46" E
23	GA	10	SPC	12	7°43'37" N, 36°43'42" E
24	GA	12	SPC	8	7°43'31" N, 36°43'17" E
27	GA	24	SPC	12	7°45'51" N, 36°43'35" E
31	GA	9	SPC	8	7°43'34" N, 36°45'29" E
FETCHE	F	>100	SFC	49	7°42' N, 36°46' E
QACHO	G	>1000	FC	65	7°46' N, 36°17' E
AFALO	G	>2000	FC	74	7°38' N, 36°13' E

2.2. Sampling method

2.2.1. Sampling material

Sampling a tree in a tropical rainforest requires a full search from the base of the tree to the outer canopy. To achieve this target we ascended the trees, whenever we thought necessary, by using the single rope technique (next paragraph). This climbing technique was not injurious to trees and was safe for the researcher (Perry 1978; Jepson 2003).

When the tree was considered strong enough to climb, the rope was placed in the tree with the help of a catapult. With the catapult a throw bag was shot, with a small, light rope attached to it, around a strong branch. The weight of the bag helped to position the rope and to make sure the rope returned to the ground. The actual climbing rope, which was too heavy to shoot directly into the canopy, was then used to replace the small rope. On this rope we climbed using the single rope technique; shunts were used that can be pushed up the rope, when they do not experience a downward force. When a downward force is applied, the shunt locks, thus holding the climber's weight. Via the use of a foot loop, working on the same principle, the climber was able to climb up the rope. For the descent the climber changed the climbing technique while hanging on a lifeline. Then a combination was used of a reverso with a shunt (Fig. 10A).

This technique made it possible to climb almost any tree of any height (Fig. 10B). The material was easy to install and to carry, saving time and man force. But this method also had some disadvantages; there was a restriction considering the supportive capacity of selected trees (Perry 1978). Branches needed to be chosen and tested carefully before the climber could safely begin. Special training was required before actual use and the climber was more or less confined to a stationary lifeline, narrowing the sampling possibilities.

Fig. 10A: Combination of shunt and reverso for descending the tree. **B:** Trees of up to 32 meters were climbed and sampled.

Only the writer of this thesis has climbed and sampled the trees. This has the advantage that the sampling of all the trees has been done by the same person ensuring less variation in counting method. In most cases, the trees were sampled from one point in the tree but sometimes it was necessary to move to other parts in the tree. This was possible by using the same rope or by shooting a second rope at another branch in the same tree. When a new species was found, samples were taken, whenever possible, for identification and for a digital herbarium. The researchers also used binoculars, a Kite Bonelli (10x42) and Kite Petrel (10x42), to observe orchids while hanging in the tree or sampling from the ground.

2.2.2. Sampling of the trees

Mature canopy trees were sampled in each fragment to measure epiphytic orchid diversity. Tree distance to the forest edge (DTE, in m) was measured to assess the effect of forest edge on distribution of epiphytic orchids. For trees located more than 100m from the edge, DTE was recorded as >100m. Since trees in close vicinity of each other tend to have a similar epiphyte flora due to the clumped distribution of many epiphyte species, trees standing well apart, separated by at least 25 meters and with crowns not overlapping, were selected (Gradstein *et al.* 2003). The height of the tree (H, in m) was defined by measuring the length of the climbing rope and/or through visual estimation.

We preferably selected older and larger trees to maximize the information on orchid diversity. They are usually richer in epiphytic orchids since the orchids had more time to colonize, and the crowns of the trees are more diverse causing a larger gradient in microclimatic conditions (Gradstein *et al.* 2003; Krömer 2003). Also, bark and canopy structure can have a strong influence on species diversity and composition of epiphytes. Therefore, we tried to sample tree species of different genera or families and we tried to maximize tree species diversity in every sampled fragment (Krömer 2007).

To document the habitat of the epiphytic orchids, the following characteristics of the host tree were measured:

1) Tree height (H)
2) Tree circumference at breast height (CBH, in cm) or height above buttresses
3) Vertical tree zone according to Johansson (1974) (see below and Fig. 11)
4) Estimation of fern species, found as epiphytes in the tree (FERNS)

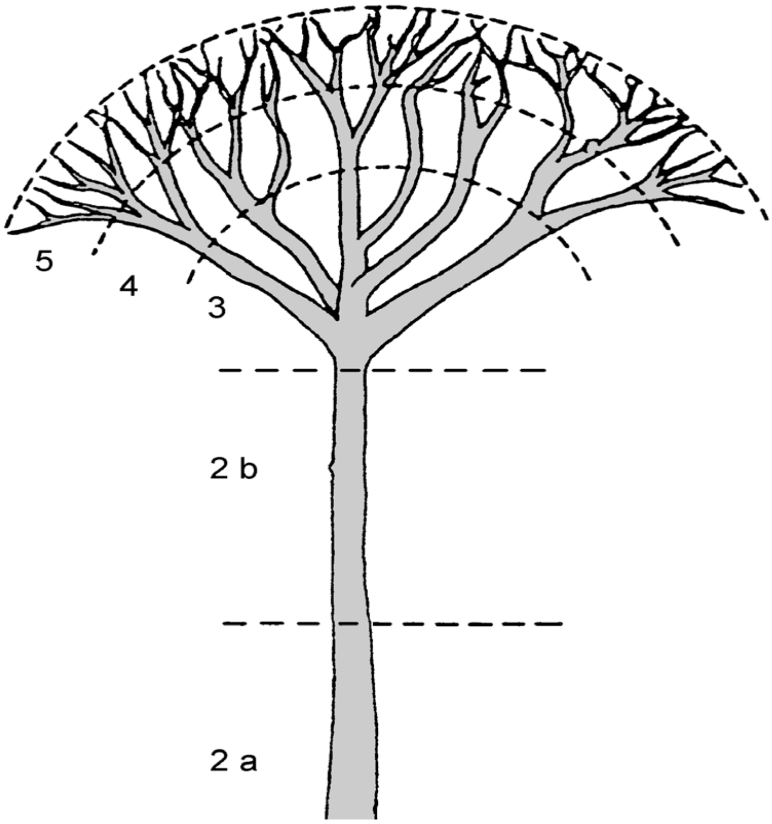

Fig. 11: Z1: trunk base, Z2a/b: lower/upper part of the trunk, Z3: lower canopy, Z4: middle canopy, Z5: outer canopy (Johansson 1974).

Each sampled tree was schematically divided into five height zones for sampling (Johansson 1974, Fig. 11): zone 1, which ranges from 0 to 1.5m above ground; Zone 2 from 1.5m above ground to the first major ramification; Z3 from the first to the second ramification; Z4 the middle crown and Z5 the outer crown. Species richness and abundance of epiphytic orchids was determined for each tree zone.

2.2.3. Sampling of the shrubs

Around the randomly chosen tree, a plot of 10m by 10m was established. Within this plot the understorey shrubs and treelets (<10m in height and >5cm in CBH) were sampled (Gradstein *et al.* 2003). The number of shrubs (n° of shrubs) per plot was noted and used as an environmental variable. The CBH of every shrub was measured, the species name was noted and the trunks were surveyed for the presence of epiphytic orchids. Species number and the number of stands for every orchid were recorded. In total, almost 10 000 shrubs were measured and inspected.

2.3. Orchids species and stands

It was difficult to count the individual orchid plants on trees to measure the actual abundance of orchid species. It was sometimes hard, especially in the larger trees, to determine where one individual epiphyte ended and the other began. Many epiphytic orchids formed mats of pseudobulbs connected by, sometimes, long rhizomes. This resulted in large masses of orchids. For this reason we used the "number of stands" in a tree as a measure of abundance. We considered a stand as *"a collection of individual stems and/or plants spatially separated from another group of the same species either by an area on the tree devoid of orchids or occupied by another species"* (Sanford 1968). Whenever an intermingling of more than one species occurred in the same area on the tree, one stand was counted for each species present (Sanford 1968). Of course this is still open to interpretation and for that reason always the same person counted the orchids in the trees.

For the correct identification of the orchid species, it is important and often necessary to inspect the flowers of the species. Without the flowers some species can be difficult to distinguish from each other (see Results). When correct identification was not possible, we identified up to genus level (Table 2). Species were identified using the Field guide to Ethiopian orchids (Demissew et al 2004) and species identity was confirmed on digital photographs by P. Cribb of the Royal Botanical Garden at Kew. Epiphytic orchids were recorded by codes (A, B, C, etc.) in the field to avoid confusion and facilitate the sampling. This combination of richness values and abundance values gives a good estimation of the orchid communities present at the sampling sites.

2.4. Data analysis

For several reasons we decided to add the observations of the Fetche site to the Garuke site. This allows us to make a direct comparison between two forest types**:** the fragmented forests (sites Garuke and Fetche, 200 plots) vs. the continuous forests (site Gera, 139 plots).

2.4.1. Summary statistics

First, data were analysed with basic statistics. To identify differences in environmental variables (H, CBH, DTE and n° of shrubs) and epiphytic orchids between tree and shrub layer and between forest types, we calculated simple means with standard deviations (SD). Nonparametric Mann-Whitney U tests were used to statistically test for these differences. We calculated indices for species diversity for every shrub and tree plot and analysed differences in diversity of orchids between forest types with Mann-Whitney U tests. We compared alfa (α, mean number of species per plot), Chao (mean richness estimator among runs), Fisher's alfa (parameter of a fitted logarithmic series distribution), Shannon Mean (Shannon diversity index), Simpson Mean (Simpson (inverse) diversity index) and Jack Mean (First-order Jackknife richness estimator) (Colwell 2009).

2.4.2. Community analysis

Before starting the community analysis we tested for outliers in the data using Outlier analysis. Plots, more than two standard deviations away from the mean, were removed from our dataset. We analysed the abundance data of the plots with nonmetric multidimensional scaling (NMS). NMS was used to explore (dis)simmilarities in the abundance data and to investigate indirect gradients influencing species distribution (Aerts *et al.* 2006). For every NMS ordination, we used Sørensen (Bray-Curtis) as a distance measure, six starting dimensions, 40 iterations to evaluate stability and an instability criterion of 10^{-5} (McCune & Mefford 2006). NMS dimensions were calculated for both the shrub plots and the tree plots. The dimensions were tested for differences between forest types with nonparametric Mann-Whitney U tests. We calculated Spearman rank correlations between environmental variables and NMS dimensions. After Bonferroni correction, providing a corrected level of significance for multiple tests, these coefficients were evaluated. With mixed model anova's we were able to correct for non independence of the fragments, fragment was here used as a random factor. We used the environmental variables as fixed effects. We also calculated between effects but, as they were never significant and following the Akaike information criterion, we deleted them from our final models.

With Indicator species analysis (ISA) we calculated indicator values (IV) for each species and the overall average p-value. We used the variable 'forest type' as a grouping variable, so for every species, the IV for the different types was calculated. The IV ranges from zero (no indication) to one (perfect indication).

After these analyses we divided the data in two datasets: one, containing the plots of the fragmented forests and one, containing the plots of the continuous forests. Again we used NMS ordination and calculated Spearman rank correlations between environmental variables and NMS dimensions. We also used mixed model anova's to correct for non independence of the fragments.

With Cluster analysis (CA), data were clustered into groups using Sørensen (Bray-Curtis) as a distance measure and a flexible beta of -0.25 as group linkage method (Aerts *et al.* 2006). To determine the optimal number of groups in the Cluster analysis, we used ISA on each grouping variable, which is output from the CA. Indicator values for each species and the overall average p-value were calculated. The last cluster step that adds >0.05 significance to the average p-value was selected as the most informative number of clusters (Aerts *et al.* 2006).

The nonparametric multiresponse permutation procedure (MRPP) test is used for testing multivariate differences among pre-defined groups. We tested for differences in community composition between the groups (clusters) in our ISA. Again we used Sørensen (Bray-Curtis) as a distance measure. The group weighting factor was n/sum(n) (with n, the number of sample plots in each group) (Aerts *et al.* 2006). The test statistic (T) describes the separation between groups while the chance-corrected within group agreement (A) describes within-group homogeneity compared to random expectation. A=1-(observed delta/expected delta). When all items are identical within groups then A equals 1. If heterogeneity within groups equals expectation by chance, then A=0. If heterogeneity within groups exceeds expectation by chance then A<0. If there is more homogeneity within groups than expected by chance, then 1>A>0. In community ecology values for A are commonly below 0.1 (McCune and Mefford 2006).

2.4.3. Correlation of tree species with orchid richness

We used one-way ANOVA to compare diversity between tree species. Because not every tree was sampled equal times, we applied post-hoc Tukey's HSD (Honestly Significant Difference) test. This is a single-step multiple procedure, comparing all possible pairs of means, in conjunction with the ANOVA to find which trees are significantly different from each other (Linton & Harder 2007).

2.4.4. Vertical distribution of orchids

We used nonparametric Mann-Whitney U tests to compare orchid abundance in the shrub layer between forest types. We used t-tests, independent by groups, to compare the relative orchid abundance for each tree zone between forest types.

Outlier analysis, clustering, ISA, MRPP and NMS ordination were perfomed in PC-ORD (Version 5.0 for Windows, McCune & Mefford 2006). For statistical tests, we used Statistica (Version 8.0 for Windows), except for the mixed models, which were run in SPSS (Version 18.0 for Windows, IBM, SPSS Inc., Chicago, IL). Diversity indices were calculated with EstimateS (Version 8.2.0, Colwell 2009).

3. RESULTS

3.1. Summary statistics

The 34 days of fieldwork resulted in data for 339 plots. It was possible to sample around ten trees a day. Twenty-two identifiable orchid species were found in the 339 sampled plots (Table 2, species list; Appendix A, digital herbarium). One species we found, was probably *P. bennettiana* but it differs from *P. rivae* only by the lip of the flower being as broad as or broader than long. When these species are found, flowering is required to ensure correct identification (Demissew *et al.* 2004). Most individuals we found of this species are probably *P. bennettiana* as this species is considered to be more widespread and common. For scientific names of orchid and tree species (Appendix A & B) we used the IPNI database (IPNI 2011).

Table 2. Epiphytic orchid species found during the sampling period (digital herbarium, see Appendix A). F=Fragmented forest, C=Continuous forest, T=Tree layer, S=Shrub layer

Sp. Code	Scientific name	Distribution
A	*Aerangis brachycarpa*	F&C, T&S
B	*Rhipidoglossum adoxum*	F&C, T&S
C	*Microcoelia globulosa*	F&C, T&S
D	*Aerangis luteo-alba*	F&C, T&S
E	*Polystachya bennettiana/rivae*	F&C, T&S
F	*Diaphananthe tenuicalcar*	F&C, T&S
G	*Diaphananthe candida*	F&C, T&S
H	*Polystachya cultriformis*	C, T&S
J	*Polystachya steudneri*	F&C, T&S
L	*Bulbophyllum josephi*	F&C, T&S
M	*Bulbophyllum intertextum*	C, T
O	*Polystachya eurychila*	F&C, T
P	*Polystachya caduca*	F&C, T&S
Q	*Diaphananthe fragrantissima*	C, T
R	*Stolzia repens*	C, T
S	*Stolzia grandiflora*	C, T
T	*Bulbophyllum* sp.	F, T
U	*Diaphananthe rohrii*	F,T
W	*Aerangis thomsonii*	C, T
X	*Polystachya tessellata*	C, T
Y	*Polystachya* sp.	C, T&S
Z	*Angraecum humile*	C, T&S

3.1.1. Descriptive statistics

Every orchid species we found in the shrubs was also found in the trees, but not vice versa. Thirteen identifiable orchid species were found in the shrub layer of the sampled plots; nine of these species in Garuke, seven in Fetche and all thirteen in Gera. This means that every orchid species in the shrub layer of both Garuke and Fetche was also found in Gera. In the plots of the tree layer, we found eleven identifiable orchid species in Garuke, nine in Fetche and twenty in Gera. Every orchid species in the tree layer of Garuke was also found in Gera. Two orchid species, *Diaphananthe rohrii* and a *Bulbophyllum* sp., were only found in Fetche. The flowering period of many of the orchid species did not coincide with our stay in the field**:** only nine of the twenty-two identified species have been found flowering during the sampling period (mid August till mid November).

Of the 339 plots we sampled for epiphytic orchids, 298 shrub plots (87.6%) and 295 trees (87.0%) supported at least one orchid species. The trees were also screened for ferns and in 11 trees (3.2%) neither orchids nor ferns were found. Abundant and widespread species included *Rhipidoglossum adoxum* and *Microcoelia globulosa* in the shrub layer and *Polystachya bennettiana/rivae* and *Diaphananthe tenuicalcar* in the tree layer (Table 3).

Table 3. Descriptive statistics: Tree <--> Shrub layer

	Trees sampled Valid N=339	**Shrub plots sampled** Valid N=339
Most abundant orchids (stands)	*P. bennettiana/rivae* (4625) & *D. tenuicalcar* (1882)	*R. adoxum* (3058) & *M. gobulosa* (2071)
Most common orchids (% plots)	*P. bennettiana/rivae* (63%) & *M. gobulosa* (36.5%)	*R. adoxum* (70%) & *M. gobulosa* (50.5%)
Mean n° of spp.	2.85 ±2.18 SD	2.35 ±1.46 SD
Min/max n° of spp.	0/10	0/6

Differences in means of biotic and environmental variables are found in table 4. The percentage of trees without orchids was much higher in the fragmented forests while the mean number of species found in a tree in the continuous forest was almost dubble of a tree in the fragmented forest. When we statistically compared the environmental variables between the forest types (Mann-Whitney U tests) we found that trees were significantly lower in the fragmented forest (Z adjusted=-5.883, p<0.001) while the CBH of the trees did not differ (Z adjusted=0.778, p=0.437). In the continuous forest, plots were further from the edge (Z adjusted=-12.492, p<0.001). Interestingly, no significant difference was found in the number of shrubs per plot (Z adjusted=0.708, p=0.479).

Table 4. Descriptive statistics: Fragmented <--> Continuous forest

	Fragmented forests Valid N=200	**Continuous forest** Valid N=139
% Trees without orchids	20%	3.6%
% Shrubs without orchids	12%	13%
Mean n° of spp. in tree	2.06 ± 1.66 SD	4 ±2.33 SD
Mean n° of spp. in shrub plot	2.34 ±1.41	2.35 ±1.54
Mean H (m)	13.28 ±3.7	16.68 ±5.6
Mean CBH (cm)	239.4 ±115.1	236.9 ±121.3
Mean n° of shrubs/plot	30 ±11.75	28.6 ±11.9
n° of tree spp.	24	27

3.1.2. Diversity statistics

The expected number of species (Mao Tau, Colwell *et al.* 2004) given the empirical data was 13 (±0.69 SD) for all the samples of the shrub layer, with 9 species (±0.0 SD) in the fragmented forests and 13 (±0.69 SD) in the continuous forest. For the tree layer, the expected number of species was 22 (±2.42 SD) for all the samples, with 14 species (±2.41) in the fragmented forests and 20 (±1.34 SD) in the continuous forest (Fig. 12).

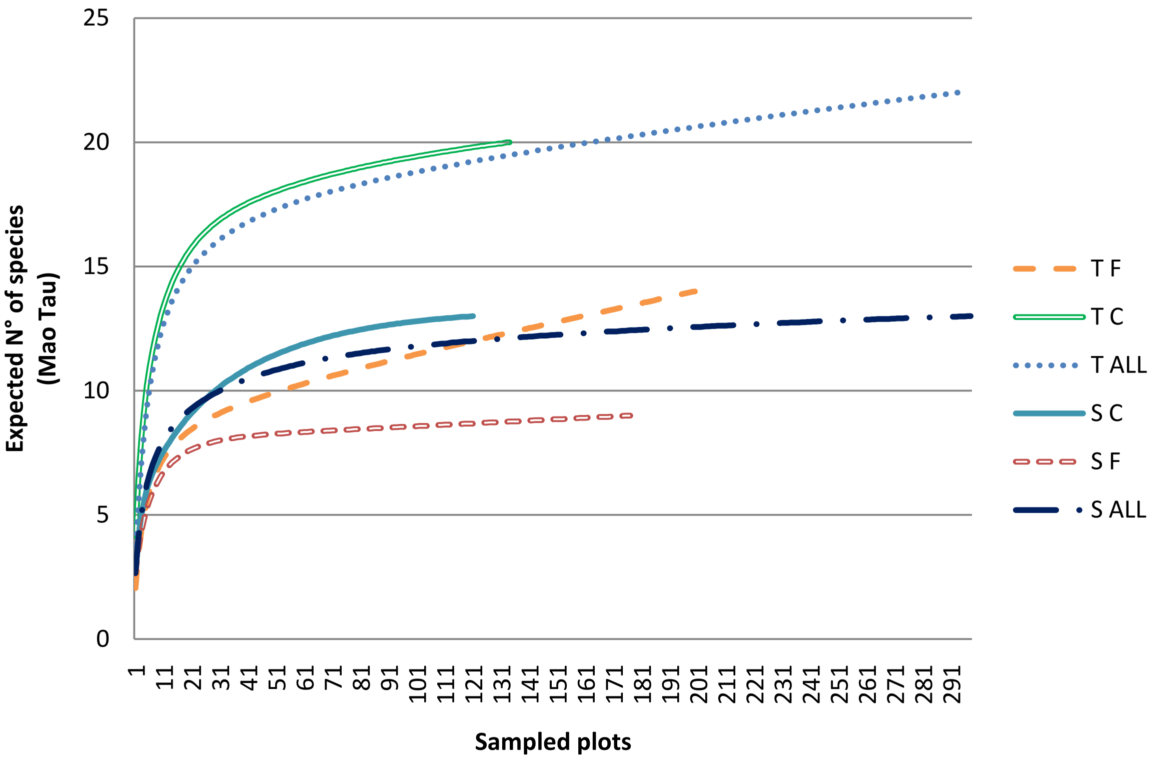

Fig. 12: Species accumulation curves: number of sampled plots against expected number of species. F=Fragmented forest, C=Continuous forest, T=Tree layer, S=Shrub layer.

We compared different diversity indices between the forest types (Table 5) with Mann-Whitney U tests. For both the tree and shrub plots, almost all diversity indices pointed to a lower diversity in the fragmented forests. Only α-diversity in the shrub layer did not differ between forest types.

Table 5. Results of Mann-Whitney U tests between forest types on diversity indices

	Shrubs: Frag. (N=177) **<--> Cont.** (N=119) **forest**		**Trees: Frag.** (N=200) **<--> Cont.** (N=132) **forest**	
	Z adjusted	*p*	*Z adjusted*	*p*
α	0.00	1.000	-7.739	<0.0001
Fisher's α	-14.554	<0.0001	-14.937	<0.0001
Chao	-12.247	<0.0001	-13.838	<0.0001
Jack	-12.836	<0.0001	-13.871	<0.0001
Shannon	-13.493	<0.0001	-10.001	<0.0001
Simpson	2.888	0.004	13.954	<0.0001

We also compared diversity indices between the forest layers (Table 6). For the plots of both the fragmented and the continuous forests, almost all diversity indices pointed to a lower diversity in the shrub layer. Only α-diversity was higher for the shrub layer in the fragmented forests.

Table 6. Results of Mann-Whitney U tests between forest layers on diversity indices

	Fragmented: Shrubs (N=177) **<--> Tree** (N=200)		**Continuous: Shrubs** (N=121) **<--> Tree** (N=134)	
	Z adjusted	*p*	*Z adjusted*	*p*
α	3.567	0.0003	-6.847	<0.0001
Fisher's α	-16.529	<0.0001	-12.759	<0.0001
Chao	-13.245	<0.0001	-12.243	<0.0001
Jack	-14.886	<0.0001	-12.898	<0.0001
Shannon	-16.133	<0.0001	-13.096	<0.0001
Simpson	-16.452	<0.0001	-13.549	<0.0001

When we correlated mean α-diversity of the tree plots with the environmental variables, a significant correlation was found for H, CBH and DTE (Fig. 13 for H, Appendix C.1 and 2 for CBH and DTE). Correlations of environmental variables with mean α-diversity of the shrub plots was never significant, though CBH showed a marginally significant correlation (p =0.065). Finally, we compared mean α-diversity of ferns between forest types, a significant lower diversity was found in the fragmented forest type (Zadj.=-2.34, p=0.022) (Boxplot in Appendix C.4).

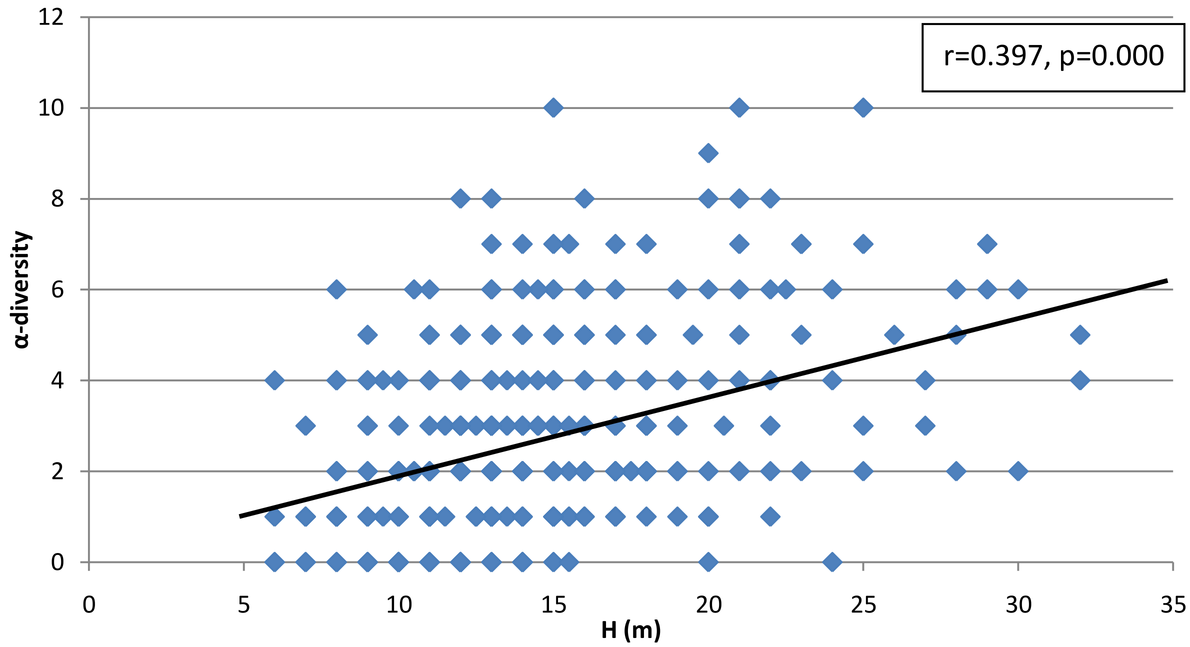

Fig. 13: Correlation between height of the tree and α-diversity of orchids in the tree.

3.2. Community analysis

The community analysis was done on plots containing one or more epiphytic orchids. This resulted in a dataset of 294 plots for the tree layer and 298 plots for the shrub layer.

3.2.1. Community analysis of the tree layer

For NMS ordination on all plots of the tree layer, the greatest reduction in 'stress' was achieved with a three-dimensional solution. The proportions of variance (coefficients of determination R^2 for the correlations between ordination distances and Sørensen distances in the original 40-dimensional space) represented by the three axes were 0.316, 0.149 and 0.109 respectively (cumulative R^2=0.573). If we look at the distribution of the plots in the NMS ordination, two groups can be distinguished, representing the two forest types; on one side, the plots of the continuous forests and on the other side, the plots of the fragmented forests (Fig. 14). Plots, close to each other in the ordination, have a similar species composition.

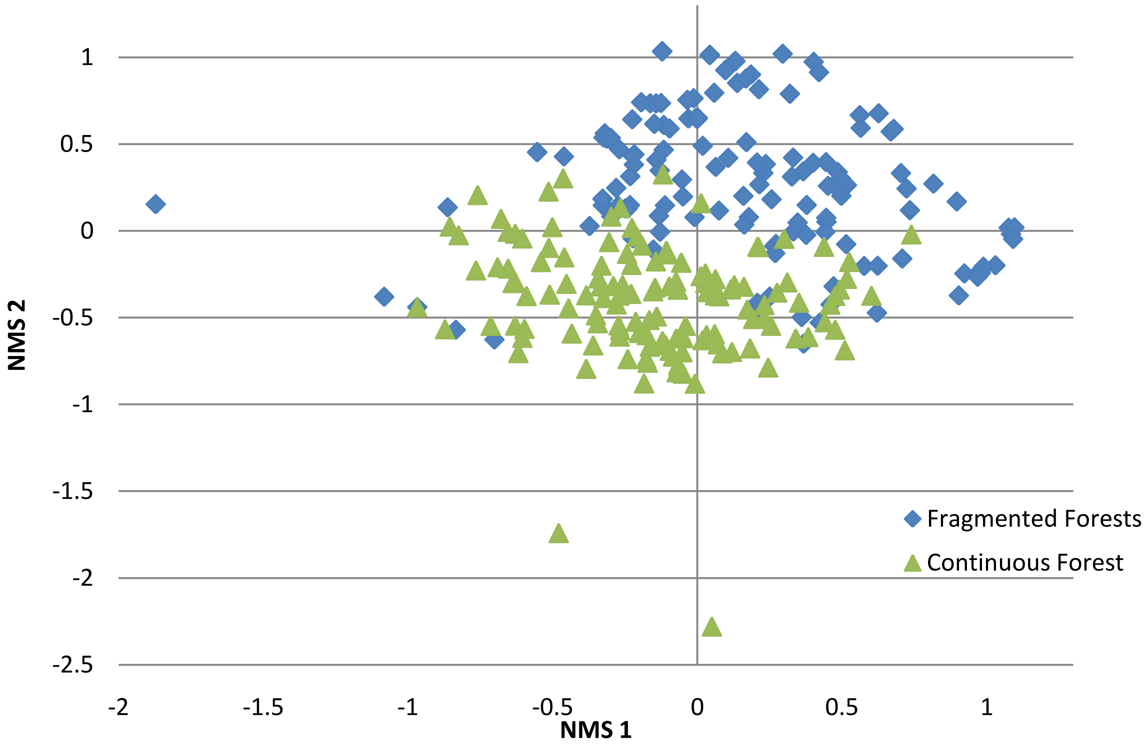

Fig. 14: NMS ordination on tree plots, different colors for the different forest types. Plots, close to each other, have a similar species composition.

We tested for differences in orchid communities between forest types by performing Mann-Whitney U tests on the NMS dimensions. For all three dimensions, a signifcant difference was found between forest types (Table 7).

Table 7. Results of Mann-Whitney U tests between regions on NMS scores

	Trees: **Frag.** (N=160) **<--> Cont.** (N=134) forest		**Shrubs:** **Frag.** (N=177) **<--> Cont.** (N=121) forest	
	Z adjusted	*p*	*Z adjusted*	*p*
NMS 1	12.259	<0.0001	-11.045	<0.0001
NMS 2	5.186	<0.0001	8.541	<0.0001
NMS 3	-6. 959	<0.0001		

We correlated the NMS dimensions with the measured environmental variables with Spearman Rank correlations. Plots were partitioned along the first NMS dimension (NMS 1) following a decreasing H, DTE and Area. Further partitioning along the second NMS dimension followed a decreasing DTE and Area but increasing CBH. Along the third NMS dimension, partitioning followed a decreasing CBH but increasing H, Area and DTE. After Bonferroni correction, the correlation with H was marginally significant (Table 8).

Table 8. Spearman rank correlations between Tree NMS plot scores and environmental variables. Valid N = 294

	NMS 1		NMS 2		NMS 3	
	r_s	p	r_s	p	r_s	p
H (m)	-0.310	<0.001	0.082	0.159	0.144	0.013
DTE (m)	-0.574	<0.001	-0.192	0.001	0.276	<0.001
CBH (cm)	-0.069	0.241	0.225	<0.001	-0.156	0.007
Area (ha)	-0.729	<0.001	-0.211	<0.001	0.338	<0.001

Correlations need to be evaluated against α_{corr}=0.0125 (Bonferroni correction for 4 tests)

We used mixed model ANOVA to correlate environmental variables to NMS dimensions and correct for non-independence of the fragments. Although all variables were influenced, fragment area and DTE were influenced the most by fragment identity. Still, we found significant correlations between NMS scores and all environmental variables (Table 9). Plots were partitioned along the first NMS dimension (NMS 1) following a decreasing CBH and Area. Further partitioning along the second NMS dimension followed an increasing CBH and H. Along the third NMS dimension, partitioning followed a decreasing CBH but increasing H and DTE.

Table 9. Mixed model ANOVA on Tree NMS plot scores and environmental variables. Valid N = 294

	NMS 1		NMS 2		NMS 3	
	t	p	t	p	t	p
H (m)	-0.425	0.671	2.838	0.005	2.225	0.002
DTE (m)	-0.832	0.406	-0.087	0.930	0.316	<0.001
CBH (cm)	-2.276	0.024	2.406	0.017	-3.574	<0.001
Area (ha)	-5.776	<0.001	-0.556	0.584	1.257	0.220

When we look at the NMS scores of the species found in the tree layer we can see some clustering of the species (Fig. 15). The proportions of variance represented by the three axes were 0.254, 0.205 and 0.135 respectively (cumulative R^2=0.593). Species, close to each other in the ordination, do often co-occur. With ISA we calculated the indicator value of each species for both the forest types. Indicative species are shown in Table 10.

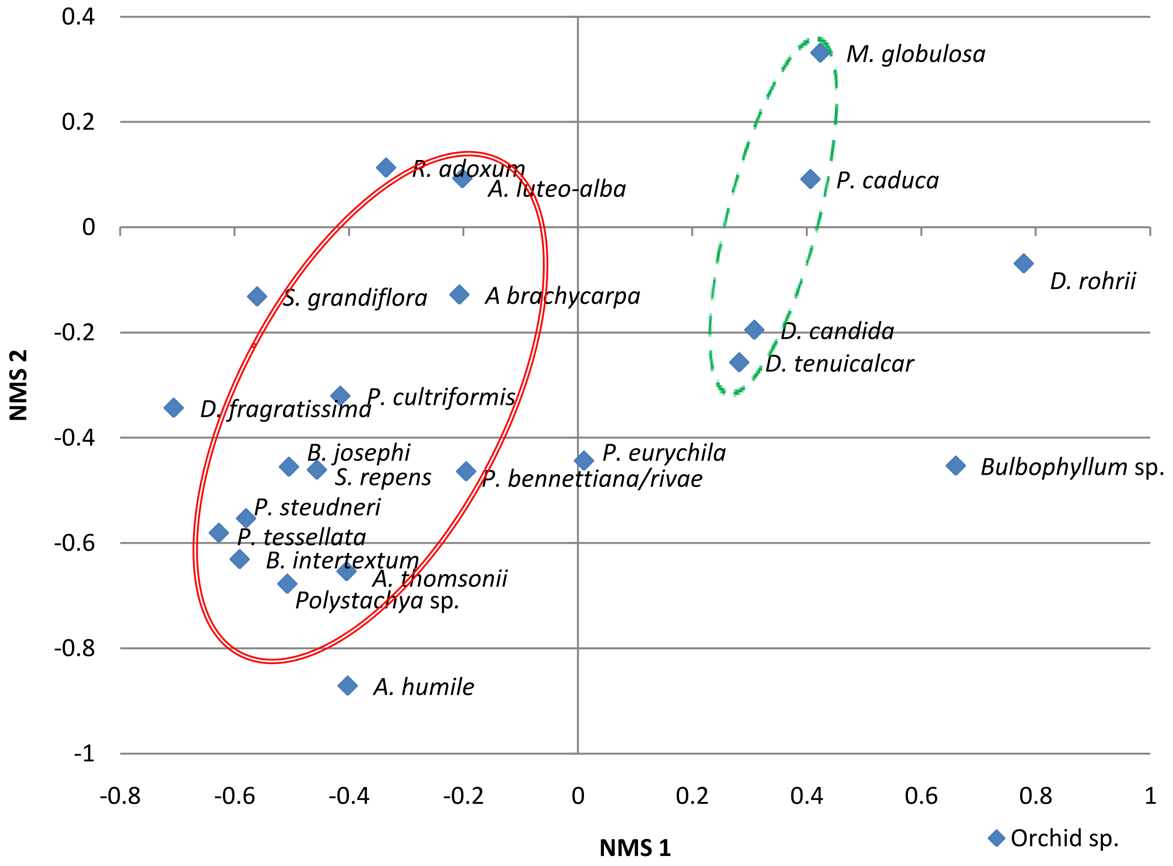

Fig. 15: NMS ordination on species in tree layer. Species, close to each other, do often co-occur. Green speckled circle: spp. indicative for fragmented forest, red dubble circle: spp. indicative for continuous forest (Table 10).

Table 10. Orchid species (tree layer) indicative for forest type, determined by Indicator species analysis

Fragmented forest	Continuous forest
Microcoelia globulosa 0.626 (0.0002)	*Polystachya bennettiana/rivae* 0.761 (0.0002)
Diaphananthe tenuicalcar 0.281 (0.0004)	*Bulbophyllum josephi* 0.444 (0.0002)
Diaphananthe candida 0.212 (0.0002)	*Polystachya cultriformis* 0.433 (0.0002)
Polystachya caduca 0.174 (0.0002)	*Polystachya steudneri* 0.326 (0.0002)
Polystachya bennettiana/rivae 0.10	*Aerangis brachycarpa* 0.269 (0.0002)
Rhipidoglossum adoxum 0.09	*Bulbophyllum intertextum* 0.237(0.0002)
	Rhipidoglossum adoxum 0.279 (0.0042)
	Polystachya sp. 0.127 (0.0002)
	Polystachya tessellata 0.097 (0.0002)
	Diaphananthe rohrii 0.075 (0.0006)
	Polystachya eurychila 0.062 (0.0252)
	Aerangis luteo-alba 0.094 (0.0784)

Spp. with their indicator value (IV) if IV>0.05. The IV ranges from 0 (no indication) to 1 (perfect indication). For observed max. IV, p-values (in parantheses) were calculated from a Monte Carlo permutation test.

3.2.2. Community analysis of the shrub layer

For NMS ordination on all shrub plots, the greatest reduction in 'stress' was achieved with a two-dimensional solution. The proportions of variance represented by the two axes were 0.363 and 0.332 respectively (cumulative R^2=0.695). If we look at the distribution of the plots on the NMS ordination, two groups are shown, representing the two forest types; on one side the plots of the continuous forests and on the other side the plots of the fragmented forests (Fig. 16).

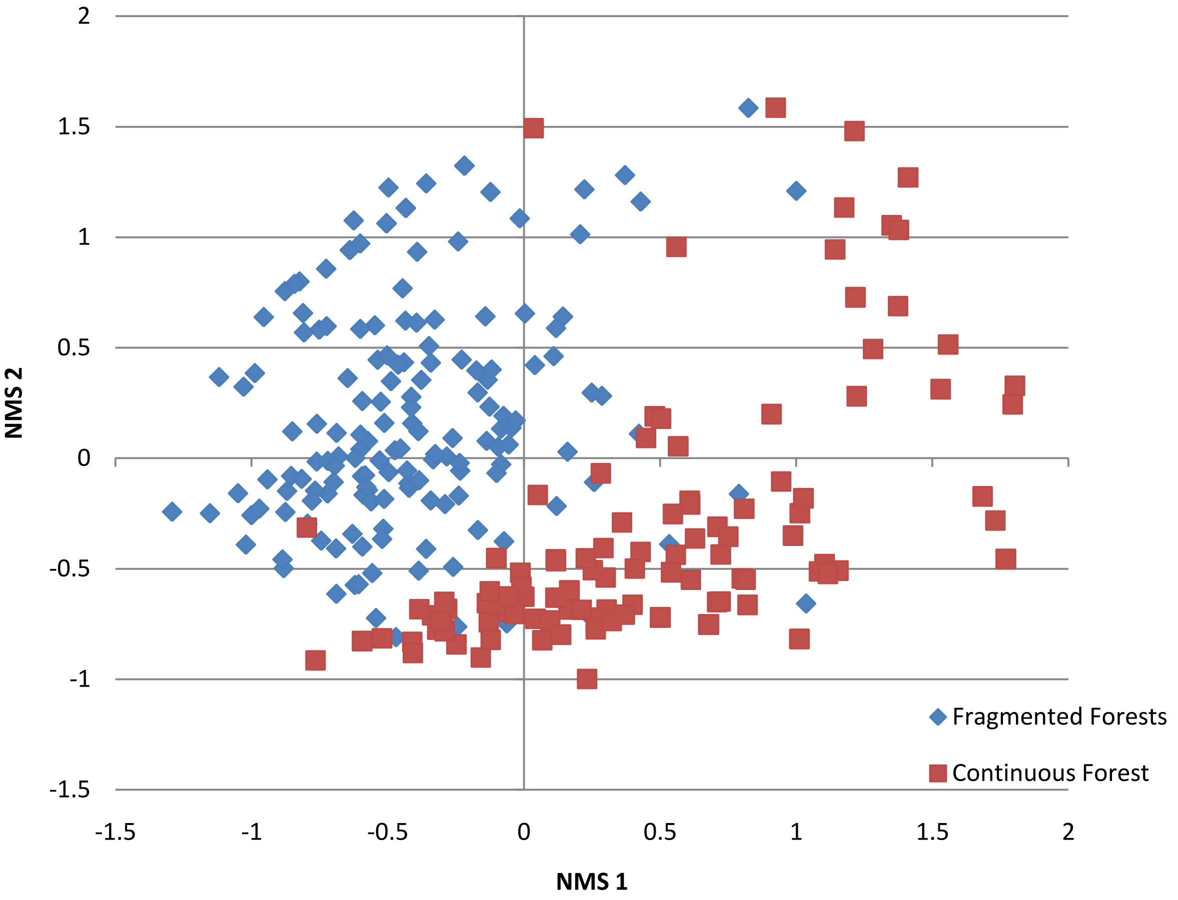

Fig. 16: NMS ordination on shrub plots, different colors for the different forest types. Plots, close to each other, have a similar species composition.

We tested for differences in orchid communities between forest types by performing Mann-Whitney U tests on the NMS dimensions. For both dimensions, a signifcant difference was found between forest types (Table 7). After Spearman correlations with environmental variables, distribution of the plots along the NMS dimensions responded to H and DTE. Plots were partitioned along the first NMS dimension following an increasing H and DTE. Further partitioning along the second NMS dimension followed a decreasing H and DTE (Table 11).

Table 11. Spearman rank correlations between Shrub NMS plot scores and environmental variables. Valid N = 298

	NMS 1		NMS 2	
	r_s	p	r_s	p
H	0.231	<0.001	-0.179	0.002
DTE	0.528	<0.001	-0.349	<0.001
CBH	-0.01	0.858	-0.008	0.888
n° shrubs	-0.015	0.791	-0.018	0.763
Area	0.552	<0.001	-0.424	<0.001

Correlations need to be evaluated against α_{corr}=0.01 (Bonferroni correction for 5 tests).

With mixed model ANOVA we corrected for non-independence of the fragments. Here, both CBH and H seemed to be the most influenced by fragment identity. For the first dimension, plots were partitioned following an increasing CBH, DTE and Area. For the second dimension, plots were partitioned following a decreasing Area (Table 12).

Table 12. Mixed model ANOVA on Tree NMS plot scores and significant environmental variables. Valid N = 298

	NMS 1		NMS 2	
	t	p	t	p
H	0.081	0.935	0.171	0.864
DTE	3.108	0.002	-0.577	0.565
CBH	2.007	0.046	-0.846	0.888
Area	3.277	0.005	-2.679	0.029

When we look at the NMS scores of the species found in the shrub layer, we can see some clustering of the species (Fig. 17). The proportions of variance represented by the two axes were 0.357 and 0.344 respectively (cumulative R^2=0.701). With ISA we calculated the indicator value of each species for both the forest types. Indicative species are shown in Table 13.

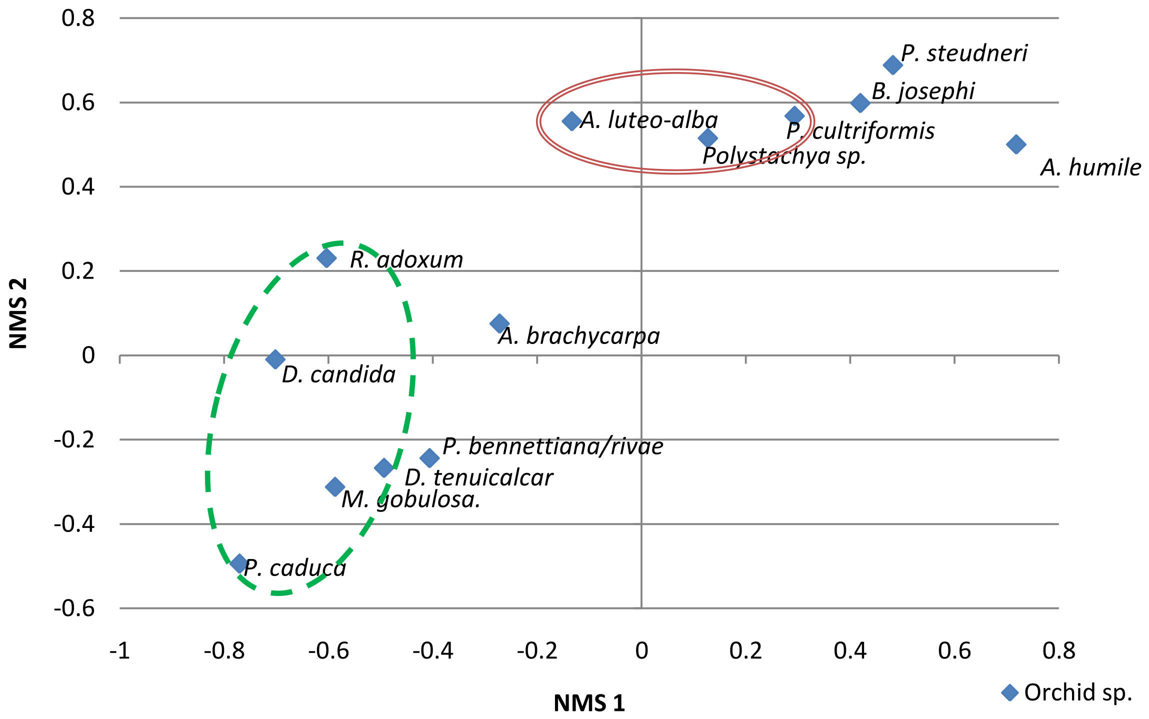

Fig. 17: NMS ordination on species in shrub layer. Species, close to each other, do often co-occur.Green speckled circle: spp. indicative for fragmented forest, red dubble circle: spp. indicative for continuous forest (Table 13).

Table 13. Orchid species (shrub layer) indicative for forest type, determined by Indicator species analysis

Fragmented forest	Continuous forest
Microcoelia globulosa 0.903 (0.0002)	*Aerangis luteo-alba* 0.40 (0.0002)
Rhipidoglossum adoxum 0.515 (0.008)	*Polystachya cultriformis* 0.358 (0.0002)
Diaphananthe tenuicalcar 0.221 (0.0002)	*Polystachya* sp. 0.058 (0.0008)
Polystachya caduca 0.079 (0.0038)	*Polystachya bennettiana/rivae* 0.172 (0.266)
Diaphananthe candida 0.062 (0.0658)	*Aerangis brachycarpa* 0.195 (0.513)
Aerangis brachycarpa 0.15	*Rhipidoglossum adoxum* 0.29
Polystachya bennettiana/rivae 0.09	

Sp. with their indicator value (IV) if IV>0.05. The IV ranges from 0 (no indication) to 1 (perfect indication). For observed max. IV, p-values (in parantheses) are calculated from a Monte Carlo permutation test for each sp.

3.2.3. Community analysis of the fragmented forest

When we explore (dis)simmilarities in the abundance data of the fragmented forests, we have the possibility to analyse the effect of fragment size on the orchid communities. The mean size of fragments in Garuke was 6.6 ha (±7.3 SD). The area of the sampled fragments ranged from 0.25 to 24 ha. When we correlated the α-diversity of plots in Garuke with the fragment size, a significant correlation was found (Fig. 18).

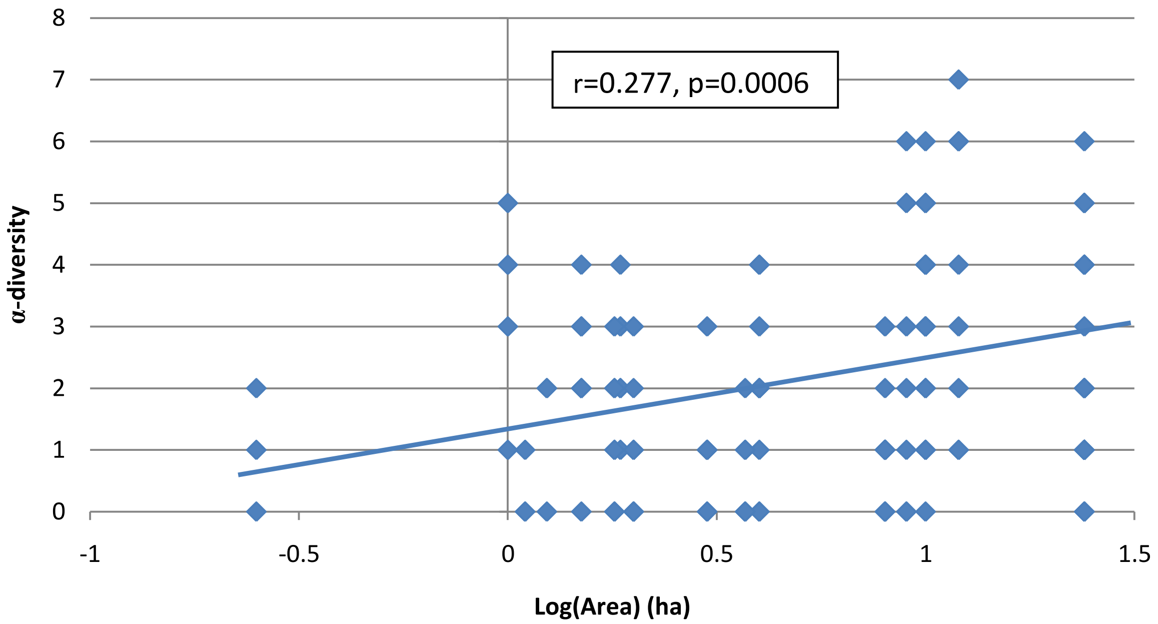

Fig. 18: Correlation between α-diversity of orchids and logarithmic transformed fragment size.

We added the observations of Fetche (fragment size c. 100 ha) to those of Garuke to analyse all the plots in the fragmented forests. We only analysed the tree plots (N=160) because shrub plots were in general very equal. We correlated the plot scores of the NMS dimensions (3 dimensions with a cumulative R^2=0.659) with environmental variables. Plots were partitioned along the first NMS dimension following an increasing fragment area and CBH. Further partitioning along the second NMS dimension followed a decreasing fragment area and DTE. After Bonferroni correction, the correlation with DTE was marginally significant. The third NMS dimension was not significantly related to the environmental variables measured in this study (Table 14). Plots from larger fragments had a higher NMS 1 score and a lower NMS 2 score and plots further from the edge had a lower NMS 2 score.

Table 14. Spearman rank correlations between Tree NMS plot scores* and environmental variables. Fragmented forest, valid N = 160

	NMS 1		**NMS 2**		**NMS 3**	
	r_s	p	r_s	p	r_s	p
H (m)	0.044	0.583	0.148	0.061	-0.061	0.445
DTE (m)	0.285	0.183	-0.194	0.014	-0.02	0.802
CBH (cm)	0.238	0.002	0.036	0.652	0.047	0.557
Area (ha)	0.311	<0.001	-0.24	0.002	0.066	0.408

Correlations need to be evaluated against α_{corr}=0.0125 (Bonferroni correction for 4 tests)
*NMS 3 showed no correlation with any environmental variable

With mixed models we corrected for non-independence of the fragments. For the first dimension, plots were partitioned following an increasing H, fragment area and CBH. Further partitioning along the second NMS dimension followed a decreasing DTE but increasing H. Along the third NMS dimension, plots were partitioned following a decreasing H but increasing CBH (Table 15).

Table 15. Mixed model ANOVA on Tree NMS plot scores and environmental variables. Fragmented forest, Valid N = 160

	NMS 1		**NMS 2**		**NMS 3**	
	t	p	t	p	t	p
H (m)	1.815	0.020	2.177	0.031	-2.240	0.027
DTE (m)	0.008	0.929	-1.864	0.064	-0.614	0.540
CBH (cm)	19.837	0.000	-1.700	0.091	2.087	<0.001
Area (ha)	9.808	0.012	0.064	0.242	1.235	0.226

3.2.4. Community analysis of the continuous forest

We also analysed the tree plots from the continuous forests (N=134) seperatly with NMS for their orchid communities. We only analysed the tree plots because shrub plots were in general very equal. We correlated the plot scores of the NMS dimensions (3 dimensions with a cumulative $R^2=0.640$) with environmental variables. We did not correlate with DTE because 88% of the plots were further from the edge than 100m (DTE=100m). Plots were partitioned along the first NMS dimension following an increasing H and CBH. Further partitioning along the second NMS dimension followed a decreasing H and CBH. After Bonferroni correction, the correlation with CBH was marginally significant. Partitioning along the third NMS dimension followed an increasing H and CBH (Table 16).

Table 16. Spearman rank correlations between Tree NMDS plot scores and significant environmental variables. Continuous forest, valid N = 134

	NMS 1		**NMS 2**		**NMS 3**	
	r_s	p	r_s	p	r_s	p
H	0.464	<0.001	-0.365	<0.001	0.223	0.01
CBH	0.357	<0.001	-0.181	0.036	0.314	<0.001

Correlations need to be evaluated against $\alpha_{corr}=0.025$ (Bonferroni correction for 2 tests)

3.2.5. Orchid communities based on cluster analysis

We used ISA on the communities of both the understorey and the canopy by labeling the plots to a forest type. With Cluster analysis (CA) and MRPP we were able to find hidden patterns in the data without labeling them. When the tree plots were clustered in three groups this provided the maximum separation between groups (T=-110.2) and a within-group level homogeneity of 0.163 (=A). Therefore, three ochid communities, containing 2–17 species, were identified in the tree layer (Appendix C.6). Clusters were internally more homogeneous than forest types ($A_{cluster}>A_{forest\ type}$) and were more separated from each other ($|T_{cluster}|>|T_{forest\ type}|$) (Table 17).

Clustering the shrub plots in three groups provided the maximum separation between groups (T=-112.8) and a within-group level of homogeneity of 0.183. Three orchid communities, containing 7-11 species, were identified in the shrub layer (Appendix C.7). Clusters were internally more homogeneous than forest types ($A_{cluster}>A_{forest\ type}$) and were more separated from each other ($|T_{cluster}|>|T_{forest\ type}|$) (Table 17).

Table 17. MRPP analysis on Cluster analysis (CA) and fores types.

Tree	**T**	**p**	**A**
Orchid communities, determined by CA and ISA, differ in species composition	-110.2	<0.001	0.163
Forest types differ in species composition	-62.7	<0.001	0.096
Shrub			
Orchid communities, determined by CA and ISA, differ in species composition	-112.8	<0.001	0.183
Forest types differ in species composition	-80.07	<0.001	0.092

3.3. Migration of orchids in respons to disturbance

With our data it was possible to analyse the possibility of epiphytic orchids to migrate from the tree to the lower stratum or to lower tree zones when disturbance in the canopy increases. We compared the data of the two forest types and indicated an increase in number of orchids in the shrub layer (3.3.1.) and a higher percentage of orchids in the lower tree zones (3.3.2.) when disturbance increased.

3.3.1. Migration of orchids to the lower stratum

In the continuous forest we sampled 3976 shrubs in 139 plots and counted 1447 orchid stands. On average 0.42 (±0.61 SD) stands per shrub were counted. In the fragmented forest we sampled 6001 shrubs in 200 plots and counted 5176 orchid stands; on average 1.03 (±1.53SD) stands per shrub were counted. With Mann-Whitney U tests, no difference was found in the number of shrubs per plot. However, the mean number of orchid stands per plot and the number of stands per shrub did differ between forest types. They were both significantly higher in the fragmented forest type. The orchid abundance in the tree layer was much higher in the continuous forest, indicating a downward migration rather than a general increase in orchid stands in fragmented forests (Table 18).

Table 18. Results of Mann-Whitney U tests between forest types

	Z adjusted	**p**
n° shrubs/plot	0.708	0.479
n° stands/plot	5.615	<0.0001
n° stands/shrub	5.313	<0.0001
n° stands/tree	-7.828	<0.0001

3.3.2. Migration of orchids to the lower tree zones

We looked at the representation of the orchids (orchid stands) in the tree zones, and found a difference between fragmented and continuous forests. In the fragmented forest, 26.4% of all orchids was found in the lower tree zones (Z2+Z3) while in the continuous forest, only 19.3% of all orchids was found in these two zones. We considered that the ecology and habitat preferences of every species is different, so we also compared representations of only the species that are shared between forest types. Now the difference was even clearer with 19.72% of all orchids in the fragmented forest found in the lower tree zones and only 10.78% in the continuous forest (Table 19).

Table 19. Representation of orchids in tree zones per forest type

Forest type	Tree zone	% all orchids	% orchids[1]
Fragmented	2	8.70%	3.42%
	3	17.50%	16.30%
	4	55.60%	76.40%
	5	18.20%	3.91%
		= 100%	=100%
Continuous	2	6.30%	1.78%
	3	13.00%	9%
	4	65.40%	79.70%
	5	15.30%	9.29%
		= 100%	=100%

[1] All orchids that are shared between the continuous and fragmented forests

When we compared the relative abundance of orchids for every tree zone between plots of the two forest types with t-tests, a significant difference was found between forest types for the higher tree zones (Z4; p=0.002 & Z5; p=0.015). However, no difference was found for the lower zones (Z2; p=0.88 & Z3; p=0.92). This showed that the vertical distribution of epiphytic orchids in the tree has shifted downwards in the fragmented forest type (Boxplots, see Appendix C.3).

3.4. Relation between epiphytic orchids and host tree species

Some studies have indicated the importance of certain tree species for conservation of epiphytes. One of the objectives was to try to indicate a difference in diversity of epiphytic orchids, depending on the tree species. Of course we only used the tree plots and only considered the tree species with five or more replicates. We seperated the plots of the fragmented forests from those of the continuous forests. This is done so because we have seen that the diversity in fragmented forest is lower so this could obscure our results. For fragmented forest, we compared mean α-diversity of orchids on the host tree species with one-way ANOVA (Fig. 19). ANOVA indicated significant differences between host tree species for orchid diversity (F=2.971, p=0.005). With post-hoc Tuckey HSD test, significant differences in diversity were only found between *Syzygium guineense* and *Croton macrostachys* (p=0.005) and between *Syzygium guineense* and *Celtis africana* (p=0.041).

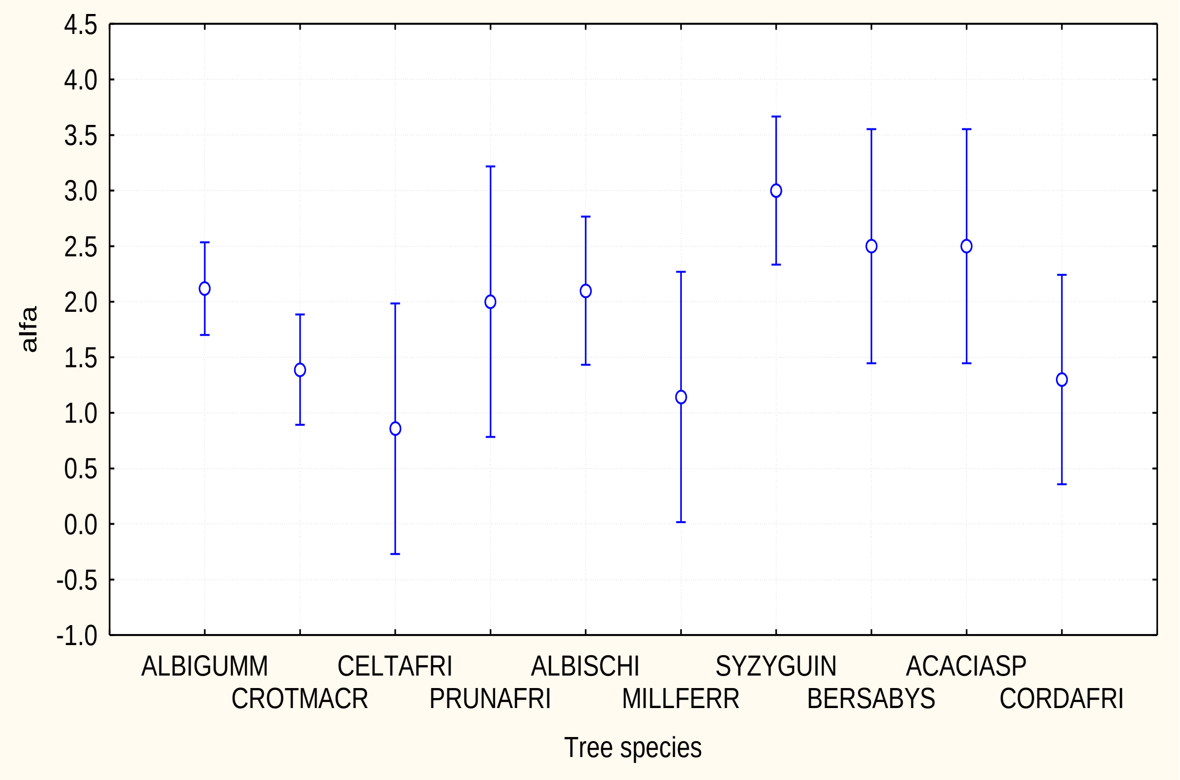

Fig. 19: ANOVA of mean α-diversity of orchids between different host tree spp. (For full name, see Appendix B) in fragmented forest. Vertical bars denote 0.95 confidence intervals.

For continuous forest, we compared mean α of the host tree species with one-way ANOVA (Fig. 20). ANOVA indicated significant differences between tree species for orchid diversity (F=6.314, p<0.001). With post-hoc Tuckey HSD test, significant differences in diversity were found between *Croton macrostachys* and respectively *Syzygium guineense* (p=0.022), *Olea welwitschii* (p=0.006), *Sapium ellipticum* (p<0.001) and *Polyscias fulva* (p=0.017). Significant differences were also found between *Sapium ellipticum* and respectively *Syzygium guineense* (p=0.032), *Schefflera abyssinica* (p=0.018) and *Ilex mitis* (p=0.01).

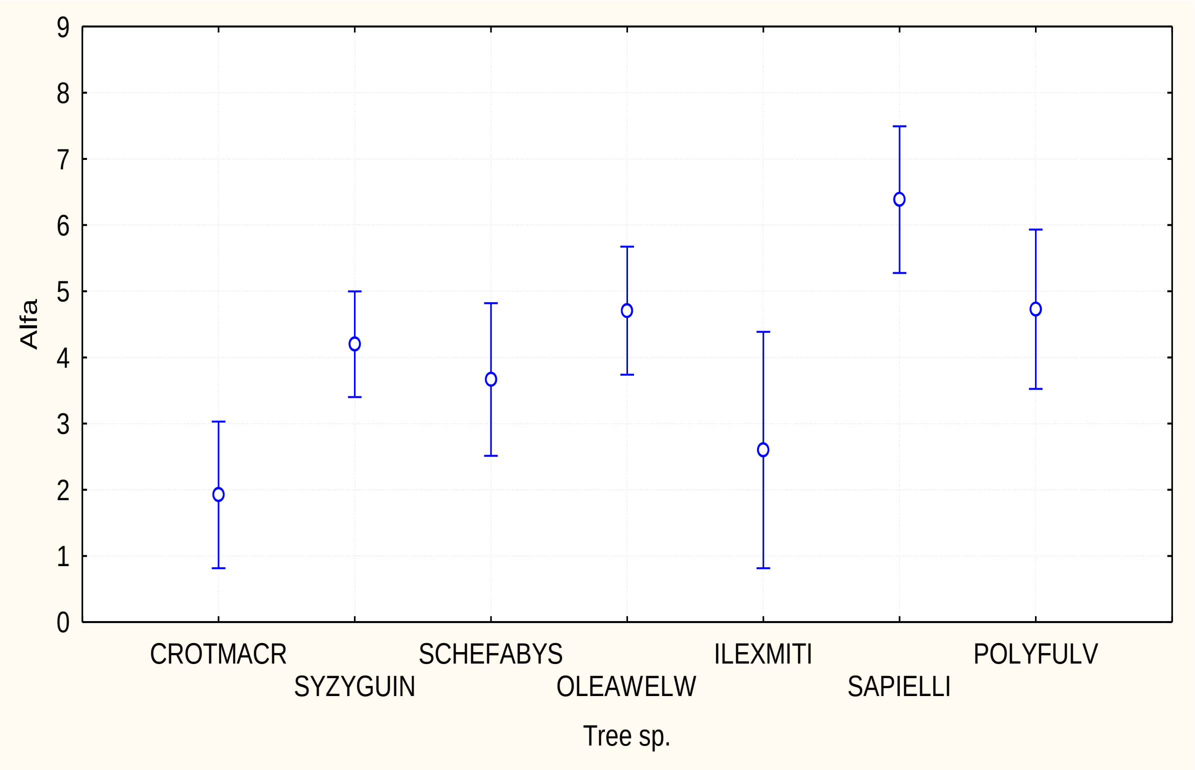

Fig. 20: ANOVA of mean α-diversity of orchids between different tree spp. (For full name, see Appendix B) in continuous forest. Vertical bars denote 0.95 confidence intervals.

We found *Sapium ellipticum* to have the highest orchid richness of all tree species while *Millettia ferruginea* was found to have the lowest orchid richness. Two tree species were sampled in high numbers in both forest types; *Croton macrostachys* and *Syzygium guineense*. *Croton macrostachys* harbored low species richness in both regions, while *Syzygium guineense* harbored rather high species richness (Table 20).

Table 20. Host tree species with their mean number of orchid species

	Fragmented forest	Continuous forest
Croton macrostachys	1.39 ±1.32 SD, N=36	1.92 ±1.50 SD, N=13
Syzygium guineense	3.0 ±2.15 SD, N=20	4.2 ±2.06 SD, N=25
	Both forest types	
Sapium ellipticum	5.5 ±2.71 SD, N=16	
Millettia ferruginea	1.11 ±0.78 SD, N=9	

4. DISCUSSION

4.1. Community and diversity analysis between forest types

We investigated the importance of pristine, undisturbed forests for orchid epiphytes by comparing the diversity of epiphytic orchids between more and less disturbed and fragmented forests. Because of the compilation of the sites Garuke and Fetche, we could only make comparisons between two forest types: continuous vs. fragmented forest. When we compared the diversity indices between forest types, all diversity indices, except one, pointed to a higher diversity in the continuous forest. The Simpson's diversity index was the only index that was higher in fragmented forests, relative to continuous forests (Table 5). In terms of sensitivity to rare species, the Simpson diversity is the least sensitive of the indices (Colwell 2009). This could explain why it is higher in fragmented forests. For both forest types, all diversity indices, except one, indicated a higher diversity in the tree layers. Interestingly, the α-diversity in the shrub layer of fragmented forests was higher than the α-diversity in the tree layer and the α-diversity between shrub layers of different forest types did not differ. This already highlights the relative importance of the shrub layer for the conservation of orchid diversity in fragmented forests. Diversity indices were only calculated in the plots containing orchid species. Because 20% of the tree plots in the fragmented forests, compared to 3.6% of the tree plots in the continuous forests were without epiphytic orchids, the diversity loss in the fragmented forests will be even bigger than what we found. Furthermore, we indicated that tree size is important for diversity of orchids. Both CBH and H showed a significant positive correlation with α-diversity.

Many studies showed that epiphytes in general are vulnerable to human disturbances (Hietz-Seifert *et al.* 1996; Barthlott *et al.* 2001; Hietz 2005; Haro-Carrión *et al.* 2009; Werner 2011). Only, several studies showed that Orchidaceae are less affected by forest disturbance compared to most other epiphyte groups (Padmawathe *et al.* 2004; Hietz *et al.* 2006; Haro-Carrión *et al.* 2009; Larrea & Werner 2010). This difference between groups is probably due to the general adaptation of epiphytic orchids to temporary dry conditions, making them less vulnerable to water stress. However, we clearly found a diversity loss in the fragmented forest type compared to the continuous forest type. We also found that the epiphytic orchid communities differed between the two forest types and this for communities in both the tree layer and the shrub layer (Table 7). The decline in diversity when forests are more disturbed by humans is in accordance with studies from the Andes, showing a loss of epiphytic orchid species in secondary vegetation compared to primary forest (Barthlott *et al.* 2001; Köster *et al.* 2009). Yet, not every study finds this diversity loss. A study of Padmawathe *et al.* (2004) in India found that large solitary trees can maintain the epiphytic orchid diversity, found in unlogged lowland forests. A study of Moorhead *et al.* (2009) in

Mexico did not find a diversity loss either, when polyculture coffee plantations were compared with natural forests. And a study of Larrea & Werner (2010) in Ecuador showed an even higher diversity of orchids in managed forests compared to unmanaged forests. These differences between studies are possibly due to the share of drought resistant and of light demanding species, present in every study area. These species will flourish when natural forests are disturbed resulting in a higher occurrence and abundance. Another possibility for the lack of decline in diversity in other studies is the possible presence of an extinction debt. Since most epiphytic orchids are perennial plants, and many species reach maturation only after 10-20 years (Schmidt & Zotz 2002), it is possible that, when forests become fragmented and cultivated, the species can still survive. It is only in the long-term that these species can become extinct, while annual plants, such as ferns, will already disappear shortly after forest disturbance.

4.1.1. Community analysis of the tree layer

For the tree layer, the plots of the fragmented forests had higher NMS 1 and 2 scores than the plots of the continuous forest type (Fig. 14, is repeated). A strong correlation was found between NMS scores and fragment size. We found that the trees in the plots of the fragmented forest type had a relatively low H. This is indicative for this forest type where the emergent trees, such as *Pouteria adolfi-friederici,* are cut. The importance of tree height as a variable to explain orchid species composition in unlogged forests in India was already shown by Padmawathe *et al.* (2004). Plots of the fragmented forest type also had a relatively low DTE, indicative for the fragmented forest where plots typically were established in smal forest fragments.

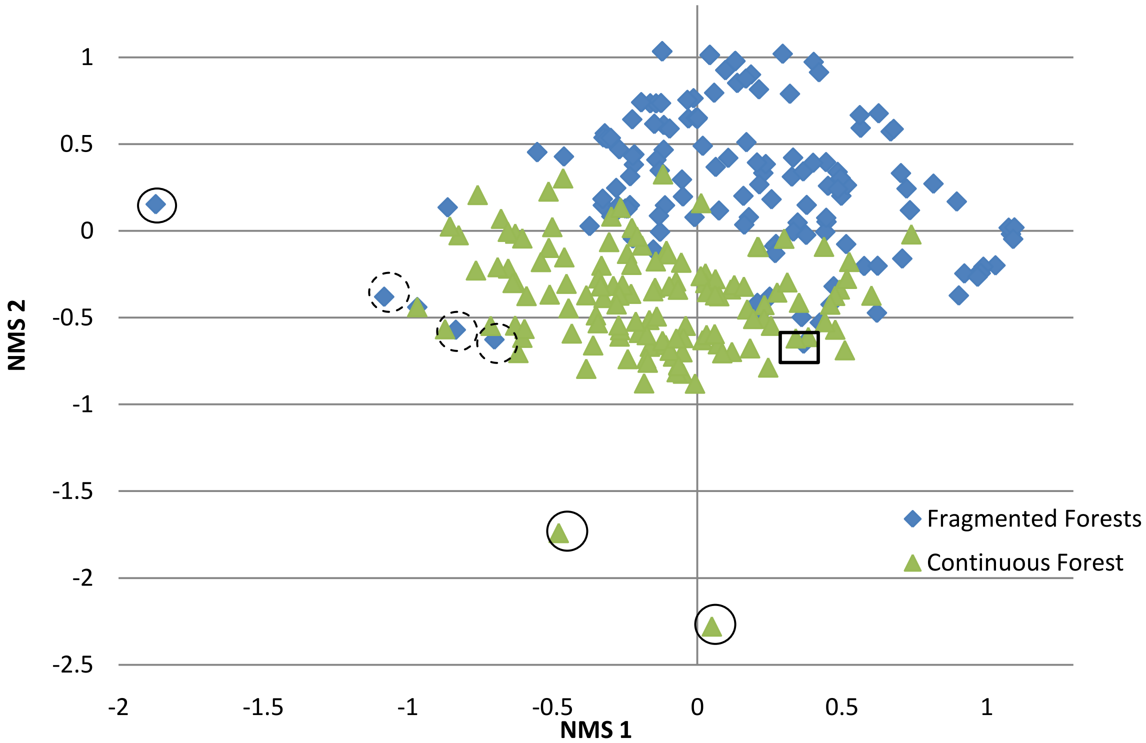

Fig. 14: NMS ordination on tree plots. See text for further details on outliers.

After correction for non-independence of the fragments with mixed model ANOVA, correlations with H and CBH were opposite of those found with Spearman correlations (Table 8, 9). We were not able to explain this sudden change in correlation. Three outliers can be found (Fig. 14, small circles) in the plot ordination. The trees in these plots harbored only one species of orchid where this orchid species normally co-occurs with other species. For the fragmented forest, three other 'outliers' could be found (interrupted circles). These plots consisted of rather small trees (≤11m) where only one single orchid species was found in the lower tree zones. This species (*Rhipidoglossum adoxum*) is much more common in the shrub layer in fragmented forests. The importance of tree heigth for orchid diversity has already been indicated in several studies for epiphyte diversity in general (Hietz 2005; Moorhead *et al.* 2009). We showed this is also the case for epiphytic orchids in specific (Fig. 13).

With ISA we were able to identify indicator species for the two forest types (Table 10). *Microcoelia globulosa*, *Diaphananthe tenuicalcar* and *Diaphananthe candida* are the most indicative species for the tree layer in the fragmented forest type. *Polystachya bennettiana/rivae*, *Bulbophyllum josephii* and *Polystachya cultriformis* are the most indicative for the continuous forest type. Not much is known on the autecology of these species. We do know that *Diaphananthe tenuicalcar* and *Diaphananthe candida* are two species that can be found in forest edges and even in wooded grasland/bushland (Demissew *et al.* 2004). This indicates that these species can survive in rather dry conditions.

Bulbophyllum josephii and *Polystachya cultriformis* are two species, typical for montane forests, which are vulnerable in Ethiopia but locally common elsewere. *Microcoelia globulosa* is found to grow on margins of evergreen forests and in secondary forests (Demissew *et al.* 2004). Its leafless appearance suggests a higher tolerance to dry conditions. In accordance with other studies, we found that drought-resistant species, such as *Microcoelia globulosa*, seem to benefit from forest disturbance (Hietz *et al.* 2006; Larrea & Werner 2010). *Microcoelia globulosa* was very rare in the continuous forest but very abundant in the fragmented forests. When it was found in the continuous forests, more than 80% of the occurrences of this species was in the outer tree zone (Z5), compared to only 27% in Z5 of the fragmented forests. Species that require more shade and/or high humidity will probably have gone extinct in the fragmented forests. Species that were only present in the continuous forests often had specific preferences. *Polystachya tessellata*, for example, is an epiphyte on trees in damp valleys and riverine forests, underlining the importance of high air humidity for this species. Many of these species have a distribution all over tropical East Africa and are quite common in other countries but some of these species are endemic to the forests of the Ethiopian Highlands. *Stolzia grandiflora*, for example, is an endemic epiphyte of Ethiopia. We only sampled this species in the continuous forest type. The species is very sensitive to habitat destruction (Demissew *et al.* 2004). This highlights the importance of the establishment of protected areas with relatively undisturbed forests in the Southwest of Ethiopia. Both the orchid species composition and the indicator species can be used to identify forest fragments of high diversity value or, the opposite, degraded forest fragments with few possibilities for diversity conservation.

Because management intensity and fragmentation are connected in this study, it was not possible to analyse them seperately to estimate the relative importance of the two factors. Nevertheless it was possible to analyse whether both factors together had an influence on orchid communities. Correlations of NMS scores of the continuous forest type with environmental variables showed that, in this forest type, tree size seems to be an important variable to explain community composition (Table 16). However, when the fragmented forest type was analysed seperately, fragment size was more important than tree size to explain community shifts (Table 14, 15). Nevertheless, CBH and H did show a significant correlation, probably due to the higher complexity of broader trees. With Spearman correlations, DTE showed a significant correlation with NMS scores but after correction for non-independence of the fragments, no significant correlation was found.

Yet, we need to be careful because larger fragments are sometimes less managed. For example in fragment 24, a large fragment (12 ha) in Garuke, we found *Polystachya eurychila*. This was the only fragment from the fragmented forest type where we sampled this orchid species. In this fragment, we also sampled a *Pouteria adolfi-friederici*. This tree species is considered as an emergent tree and was almost completely absent from the fragmented forests (we only found one individual in the fragmented forest type). The *Pouteria adolfi-friederici* was the only tree in the fragmented forest type where we found the orchids *Bulbophyllum josephi* and *Bulbophyllum intertextum*. Therefore, this tree appears between the plots of the continuous forests in the NMS plot ordination (small square on repeated Fig. 14). Because this fragment was more distant from the surfaced road than any other fragment we sampled in Garuke (Fig. 7), it is possible that it is less managed. This fragment strongly suggests that the differences we found in species composition and diversity between forest types is not a question of differences in climate or height above sea level between the study sites. Besides fragmentation, forest management is an important variable for explaining diversity patterns of epiphytic orchids. The forest in fragment 24 appears to be less managed and thus, other species can occur. Especially the canopy layer seems to be important. In the continuous forest type, there is a higher number of trees per ha, a higher heterogeneity in species, size and age classes of the trees and trees are less disturbed compared to the fragmented forest type. In the fragmented forest type, canopy thinning has resulted in the degeneration towards a species-poor forest with mostly gap and pioneer species (Senbeta & Denich 2006; Aerts *et al.* 2011).

4.1.2. Community analysis of the shrub layer

For the shrub layer, the plots of fragmented forests had lower NMS 1 and higher NMS 2 scores than plots of the continuous forest type. NMS scores were strongly correlated with Area and plots of the continuous forests were further from the edge and had a higher H (Table 11). Correction for non-independence of fragments did not change much of the correlations with the variables, although now CBH is more important to explain differences in communities than H (Table 12). With ISA we were able to analyse indicator species for the two forest types (Table 13). *Microcoelia globulosa* and *Rhipidoglossum adoxum* are the most indicative species for the shrub layer in the fragmented forest type. *Aerangis luteo-alba* and *Polystachya cultriformis* are the most indicative for the continuous forest type. These are species that occured mainly in the shrub layer or on lower tree zones because they require a lot of shade, except *Microcoelia globulosa*, which was very common in fragmented forests in both the canopy and the understorey.

Our field observations suggested the importance in fragmented forests of old coffee shrubs of medium height. These shrubs hosted the most epiphytic orchids whereas young and thin or heavy coppiced shrubs did not harbor many orchids (Appendix C.5). Field observations from a study of Hylander & Nemomissa (2008), studying epiphyte diversity on coffee shrubs in Ethiopia, showed the same pattern. Interestingly, also very broad shrubs harbored fewer orchids. These shrubs are generally higher, exposing the orchids to drier conditions. Again this highlights the influence of forest cultivation on orchid biodiversity. The old coffee shrubs generate a structural complexity below the canopy, mimicking the loss of complexity in the canopy. This is favorable for certain species but many species, sensitive to human disturbance, were not found in the fragmented forest type. Because of a more intense forest disturbance, these species are probably extinct here.

Some coffee farmers believe that epiphytic orchids are parasites and remove them from the coffee shrubs in order to avoid a coffee yield decline (Own observations, Fig. 21). A study of Hylander & Nemomissa 2008 in the same area found that farmers are concerned about epiphytes for a possible yield decline. Educating the farmers to clarify the non-parasitic status of the orchids can enhance the diversity of orchids in the shrub layer.

Fig. 21: A farmer is removing epiphytes from a coffee shrub.

In accordance with other studies, we can state that both the composition and diversity of epiphytic orchids in the understorey and the canopy can be used as indicators of human-induced disturbance in a forest landscape (Hietz *et al.* 2006; Hylander & Nemomissa 2008; Haro-Carrión *et al.* 2009).

4.1.3. Orchid communities based on cluster analysis

We analysed the plots with cluster analysis and MRPP to detect communities without labeling them in advance. Three communities were found in both layers (Appendix C.6 and C.7). Although CA was better to identify orchid communities (Table 17), communities were rather similar compared to communities based on forest types although with CA, an 'intermediate community' was found. This community assembles these plots that were rather similar in species composition but were sampeled in a different forest type. In the tree layer, one group of plots belongs to the community with only one indicative species. Most trees in these plots harbor only one species, *Microcoelia globulosa*, indicative for very disturbed plots.

In the shrub layer, communities based on CA and MRPP were not so different from communities found by ISA on forest types. Again an intermediate community was found, assembling these plots that are similar but sampled in different forest types. We can conclude that the classification of species in communities, based on labeling by forest types is not so different to the one, based on CA.

4.2. Vertical distribution of epiphytic orchids

Changes in forest microclimate through fragmentation and canopy thinning can result in a migration of orchids to lower tree zones or even to the understorey. Our results show that orchids in the fragmented forest type appear to occur lower in the trees, relative to the continuous forest type (Table 19, Appendix C.3). This is in accordance with the studie of Haro-Carrión *et al.* (2009) who found, in Ecuador, a downward shift in the vertical distribution of vascular epiphytes in plantations relative to natural forests. Also, we found an increase in the number of stands per shrub plot and per shrub in the fragmented forest type (Table 18). As most rare species were only found in the trees, the diversity was not higher but the higher number of stands indicates that the shrub layer can act as a refuge area when the tree layer gets more disturbed. This is similar to what is found in a study of Solis-Montero *et al.* (2005) in Mexico. This study showed that shade coffee plantations can act as refuge areas for epiphytic orchids. Coffee shrubs in the fragmented forest can contribute to overall species richness by increasing the area of habitat and by offering a different microclimate compared to the shade trees. This is in accordance with the studie of Hylander & Nemomissa (2008) who indicated the importance of the crop (*Coffea arabica*) as epiphyte biodiversity repository in home gardens in Ethiopia.

Thus, besides the diversity and the community composition of orchid species, the vertical distribution of the orchids can be an important indicator of forest disturbance. Moreover, in disturbed forests, the shrub layer can partially compensate for the loss of epiphytic orchids in the tree layer.

4.3. Importance of host tree species for conservation of epiphytic orchids

Our last objective was to investigate the importance of host tree species identity for epiphytic orchid diversity. Depending on the species, trees can have certain characteristics that improve the establishment and growth of epiphytic orchids. We found for both forest types that some host tree species have higher numbers of orchid species than others. Most significant differences were found between tree species in the continuous forests. This is probably because the diversity in the canopy was higher, not only with respect to the number of tree species, but also regarding the structural build-up and the age classes. Most of the fragmented forests contained only a few tree species, all of the same size and with poor variation in age classes leading to a homogenization of the forest (Schmitt 2006; Senbeta & Denich 2006).

Croton macrostachys harbored a low epiphytic orchid richness and *Syzygium guineense* a rather high richness in both forest types (Table 20). This is an indication that differences between host tree species are consistent between forest types. *Croton macrostachys* is a medium-sized tree with an open crown and a fairly smooth bark. *Syzygium guineense* is a medium-sized climax species with a dense crown and, for older trees, a rough bark (Fichtl & Adi 1994). This is a possible reason for its high orchid richness. The dense crown allows enough shading conditions, even in the fragmented forests where the canopy is more open. The rough bark probably allows epiphytic orchid seedlings to establish more easily. *Millettia ferruginea* harbored the least orchid species of all sampled tree species. The species was only represented twice in the plots of the continuous forests so no comparison between forest types could be made. Both *Croton macrostachys* and *Millettia ferruginea* are fast growing gap or pioneer species in Ethiopian Afromontane forests, typical for disturbed sites (Schmitt *et al.* 2009; Aerts *et al.* 2011). This is a possible explanation for their low orchid richness. *Sapium ellipticum* was found to be the most species-rich of all sampled tree species but was only twice represented in the plots of the fragmented forests. It is a large deciduous tree species with a large crown and a rough bark (Fichtl & Adi 1994). Again, the rough bark probably allows epiphytic orchid seedlings to establish more easily while the large crown can create broad differences in microclimate in the tree. Possibly this tree species would be beneficial to overall orchid species richness in the fragmented forest type as well. This indicates, in accordance with other studies, the importance of some host tree species for epiphytic orchids and the conservation of these tree species throughout forest types to maintain epiphytic orchid diversity (Haro-Carrión *et al.* 2009).

4.4. Limitations of the experimental design

While in the field, we came across some limitations, possibly interfering with our results. Some orchids were hard to find because of their small size (Fig. 17A) or because they were restricted to certain microzones in the tree. This implicates that some species were possibly overlooked while other species were more completely sampled. This is mainly the case in the continuous forests where trees were in general more overgrown by epiphytes, semi-epiphytes or parasites, obscurring our search for epiphytic orchids. Not every orchid species was easy to identify. When no flowers were present, we could not always identify up to species level. Moreover, some of the orchids were counted but not analysed because they were left undetermined. Therefore, species richness is believed to be higher in the sampled area than found in this study. It seems plausible that in certain circumstances, orchids were not correctly determined. This is most likely the case for *Polystachya steudneri*. The individuals we identyfied as this species possibly belonged to multiple species but because of the lack of flowers we classified the observations as belonging to one species. Orchid stands in the tree were usually much larger than stands in the shrubs, but both were counted as one (Fig. 17B). Stands in the continuous forests were often larger and more difficult to count than in the fragmented forests. This could have led to an underestimation of orchid abundance in the trees, specifically in the continuous forests.

Fig. 17A: Large hanging masses of *Diaphananthe tenuicalcar*. **B:** Very small *Angraecum humile*.

Moreover, not every tree was safe enough to climb, making random sampling more complicated. Also, not every branch was safe enough to climb, making it more difficult to sample a tree completely. Though time consuming, it would be interesting to measure more environmental variables. Measuring the canopy cover with a spherical densitometer could result in an interesting environmental variable. An evaluation of the microclimate, measuring factors such as vapor pressure deficit, air temperature and relative humidity, and an estimation of tree age could help to explain the found patterns (Gradstein *et al.* 2011). A more accurate measuring method for H (sometimes estimated) and DTE (limited to 100m) could improve our results.

4.5. Recommendations for epihytic orchid conservation

We found a clear shift in community composition and species diversity loss when coffee forests become more fragmented and cultivated, showing that alternative land use cannot compensate for pristine forests. On the other hand, still a lot of forest diversity can be found in the fragmented forests (Aerts *et al.* 2011). As reported for other managed forests, these cultivated forests obviously contributed to the conservation of epiphytic orchid diversity in the region (Hietz 2005; Haro-Carrión *et al.* 2009). Perhaps when fragmented forests are in proximity to more natural forests, source-sink populations can increase orchid diversity. The diversity could also be increased when coffee farmers would be stimulated to enhance the complexity of the coffee forests in both the shrub and tree layer. Coffee farmers should also aim for larger fragment sizes instead of the present agricultural landscape matrix. Rewarding farmers for the establishment of exclosures in their coffee forests would not only be beneficial for forest regeneration, allowing new tree seedlings to establish, but could also help as refuge areas for epiphytic orchids. For forest species in general, exclosures can aid their survival in a degraded landscape (Fig. 18) (Aerts *et al.* 2011; Goris 2011). As such, exclosures have both economical and ecological benefit.

Fig. 18: Ground orchid, *Habenaria bracteosa*, found in exclosure in the fragmented forest. This orchid was not found outside the exclosure except in the continuous forest.

Because of the high human population pressure in the area, and the fact that c. 15 million Ethiopians depend on coffee for their main income, forest conservation concepts will only work when in cooperation with local farmers (Petit 2007). A combination of poverty reduction and biodiversity conservation should be beneficial for the longterm protection of forest species and habitat. Increasing the quality of matrix habitat could benefit forest dependent species (Vandermeer & Perfecto 2007). Farmers can be compensated for possible yield loss or effort put into conservation measures. In this context it seems interesting to reward farmers with a certificate allowing them to ask higher prices for their coffee yield (Schmitt *et al.* 2009). Anyhow, establishment of biodiversity conservation hotspots, both in the fragmented and in the continuous forests should be top priority. These spots need to be chosen carefully and can maintain or even enhance the diversity of epiphytic orchids and forest species in general. For both the canopy and the understorey we have indicated a species shift from more natural to more degraded forest. This highlights the use of epiphytic orchids for conservation projects. It is an attractive group of plants, sensitive to human-induced changes, with possibilities for ecotourism. They can be used as flagship species to raise funding for research and conservation. In this way this group can protect forest ecosystems in general. The establishment of "biodiversity hotspots" can act as repository for rare species, genetic resources (wild coffee included) and as source for source-sink populations. At least one of the orchids we found, *Aerangis luteo-alba*, was threatened because of its horticultural value (Demissew *et al.* 2004).

4.6. Possibilities for future research

Future research on the distribution of epiphytic orchids in Southwest Ethiopia could focus on how to determine the relative importance of fragmentation and cultivation of the forest. These two factors are connected in this study but could be separated in a well considered experimental design. In the context of orchid diversity loss, it looks promising to explore the possibility of an extinction debt in the fragmented forests via long-term studies and data of the historical landscape. When DNA of the epiphytic orchids could be sampled it should be possible to relate genetic variation and gene flow to fragmentation and isolation. Also, it seems interesting to relate the diversity of epiphytic orchids to the diversity of other groups of epiphytes. Is the effect of forest disturbance the same for other groups or is there variation between groups?

5. CONCLUSION

This study has analysed the diversity of epiphytic orchids between two forest types; continuous vs. fragmented forests. For both the canopy and the understorey we have indicated a shift in species composition from continuous to fragmented forest. We also found a diversity loss in both the canopy and the understorey for fragmented forests. We showed that the diversity of epiphytic orchids is negatively affected by human disturbance through both fragmentation and cultivation. We showed that in both forest types, tree size is an important variable to explaine orchid communities and diversity. This indicates the importance of structural, large and old trees to maintain orchid diversity. In fragmented forests, the size of the fragment and the distance of the plot to the forest edge are more important variables to explain community differences.

We compared the data of the two forest types and indicated an increase in abundance of orchids in the shrub layer and a higher percentage of orchids in the lower tree zones when disturbance increased. Furthermore we indicated for both forest types the importance of both the size and the species of host trees for conservation of the epiphytic orchid diversity. Some host trees harbor a high orchid richness while other harbor only few species. We can conclude that, in accordance with other studies, both the composition and diversity of epiphytic orchids and their vertical distribution can be used as indicators of human-induced disturbance in a forest landscape. Indicator species and species composition can be used to evaluate the value of forest remnants for conservation of biodiversity.

We showed the importance of the epiphytic orchids for conservation efforts. We strongly support the in-situ conservation of large, undisturbed forests for long-term maintenance of the epiphytic orchid diversity, with several endemic species, in the montane rainforest of Southwest Ethiopia.

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APPENDIX

Appendix A: Identified orchid species

Aerangis brachycarpa (A.Rich.) Durand

Microcoelia globulosa (Hochst.) L.Jons

Rhipidoglossum adoxum (Rasm.) Senghas

Aerangis luteo-alba Schltr.

Polystachya caduca Rchb.f.

Diaphananthe candida P.J.Cribb

Bulbophyllum josephi M.Kumar & Sequiera

Diaphananthe tenuicalcar Summerh.

Diaphananthe rohrii (Rchb.f.) Summerh.

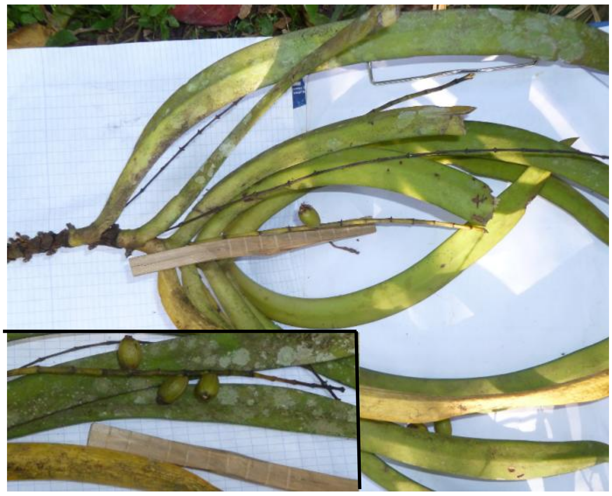
Polystachya cultriformis Lindl. ex Spreng.

Bulbophyllum intertextum Lindl.

Polystachya steudneri Rchb.f.

Stolzia grandiflora P.J.Cribb

Stolzia repens (Rolfe) Summerh.



Diaphananthe fragrantissima Schltr.

Aerangis thomsonii Schltr.

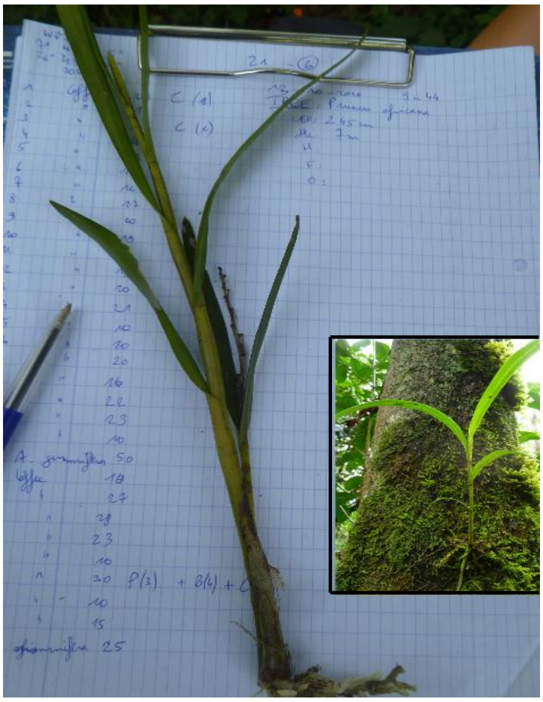
Angraecum humile Summerh.

Polystachya sp.

***Bulbophyllum* sp.**

***Polystachya tessellata* Lindl.**

***Polystachya eurychila* Summerh.**

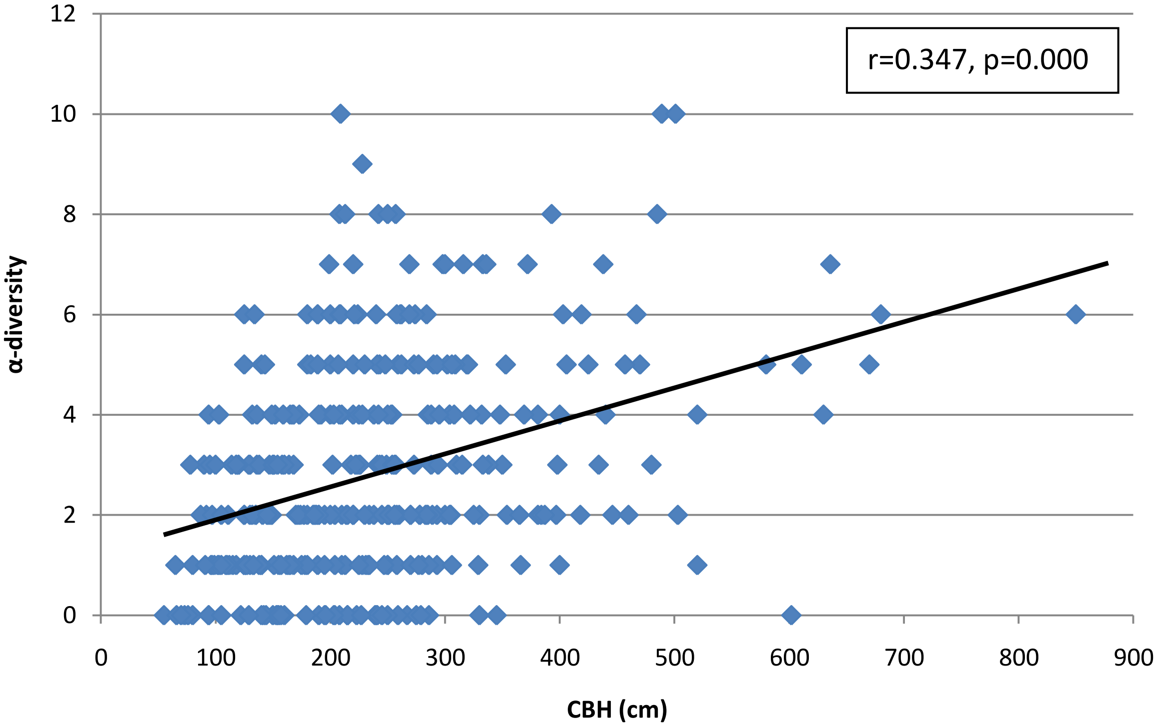


***Polystachya bennettiana* Rchb.f. / *Polystachya rivae* C.Schweinf**

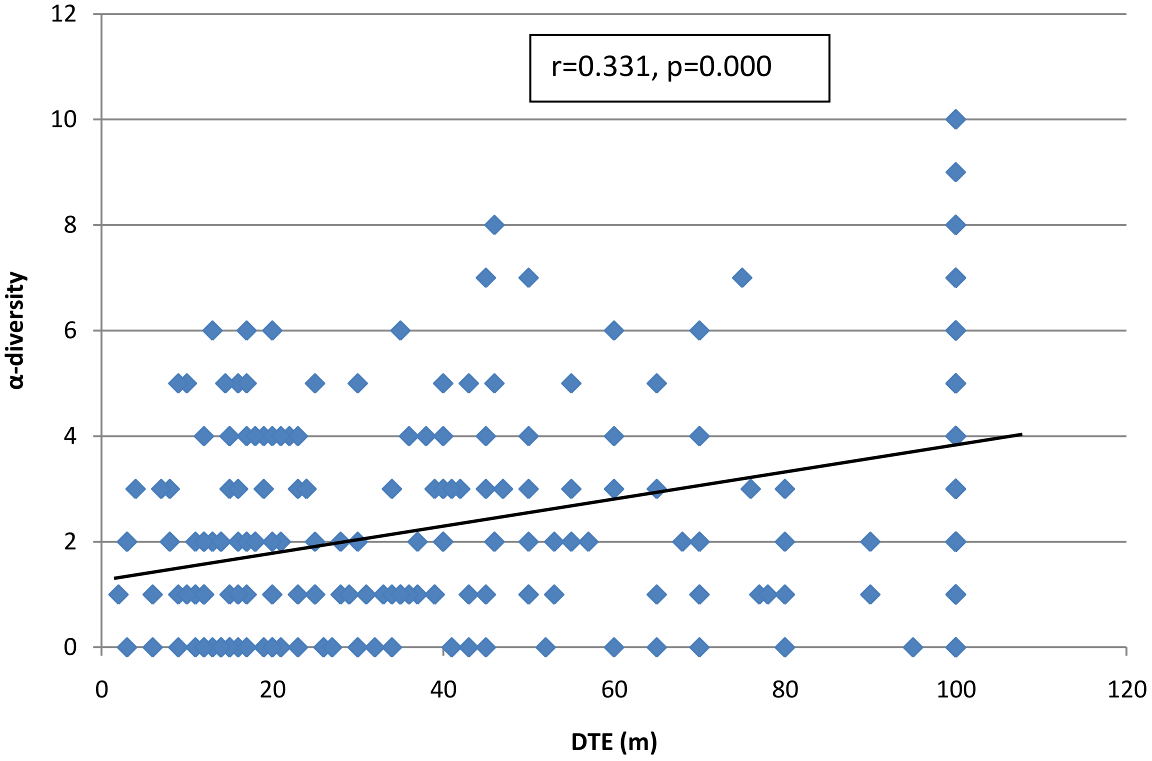
Appendix B. List of sampled tree species

SHORT	Scientific name	CODE
ALBIGUMM	*Albizia gummifera* C.A.Sm.	1
CROTMACR	*Croton macrostachys* Hochst. ex A.Rich.	2
CELTAFRI	*Celtis africana* Burm.f.	3
PRUNAFRI	*Prunus africana* (Hook.f.) Kalkman	4
ALBISCHI	*Albizia schimperiana* Oliv.	5
MILLFERR	*Millettia ferruginea* Hochst.	6
SYZYGUIN	*Syzygium guineense* Guill. & Perr.	7
AFROFALC	*Afrocarpus falcatus* (Thunb.) C.N.Page	8
SCHEFABYS	*Schefflera abyssinica* Harms	9
BERSABYS	*Bersama abyssinica* Fresen.	10
FICUVAST	*Ficus vasta* Forssk.	11
FICUSYCO	*Ficus sycomorus* L.	12
OLEAWELW	*Olea welwitschii* Gilg & G.Schellenb.	13
OLEACAPE	*Olea capensis* Buchoz ex Roem. & Schult.	14
ILEXMITI	*Ilex mitis* Radlk.	15
DRACSTEU	*Dracaena steudneri* Engl.	16
POUTADOL	*Pouteria adolfi-friederici* (Engl.) Baekni	17
MACACAPE	*Macaranga capensis* Sim	18
SAPIELLI	*Sapium ellipticum* Pax	19
TECLNOBI	*Teclea nobilis* Delile	20
POLYFULV	*Polyscias fulva* Hutch. & Dalziel	21
ACACIASP	*Acacia* sp.	22
CORDAFRI	*Cordia africana* Lam.	23
MIMUKUMM	*Mimusops kummel* Bruce ex A.DC.	24
DIOSABYS	*Diospyros abyssinica* (Hiern) F.White	25
FICUTHON	*Ficus thonningii* Blume	26
CASSMALO	*Cassipourea malosana* Alston	27
EUPHAMPL	*Euphorbia amplophylla* Pax	28
ALLOABYS	*Allophylus abyssinicus* Radlk.	29
MAYTADDA	*Maytenus addat* (Loes.) Sebsebe	30
Species Y		31
BERSABYS + FICUVAST		32
Species X		33
SCHEFABYS + SAPIELLI		34
Anonu (orom.)		35

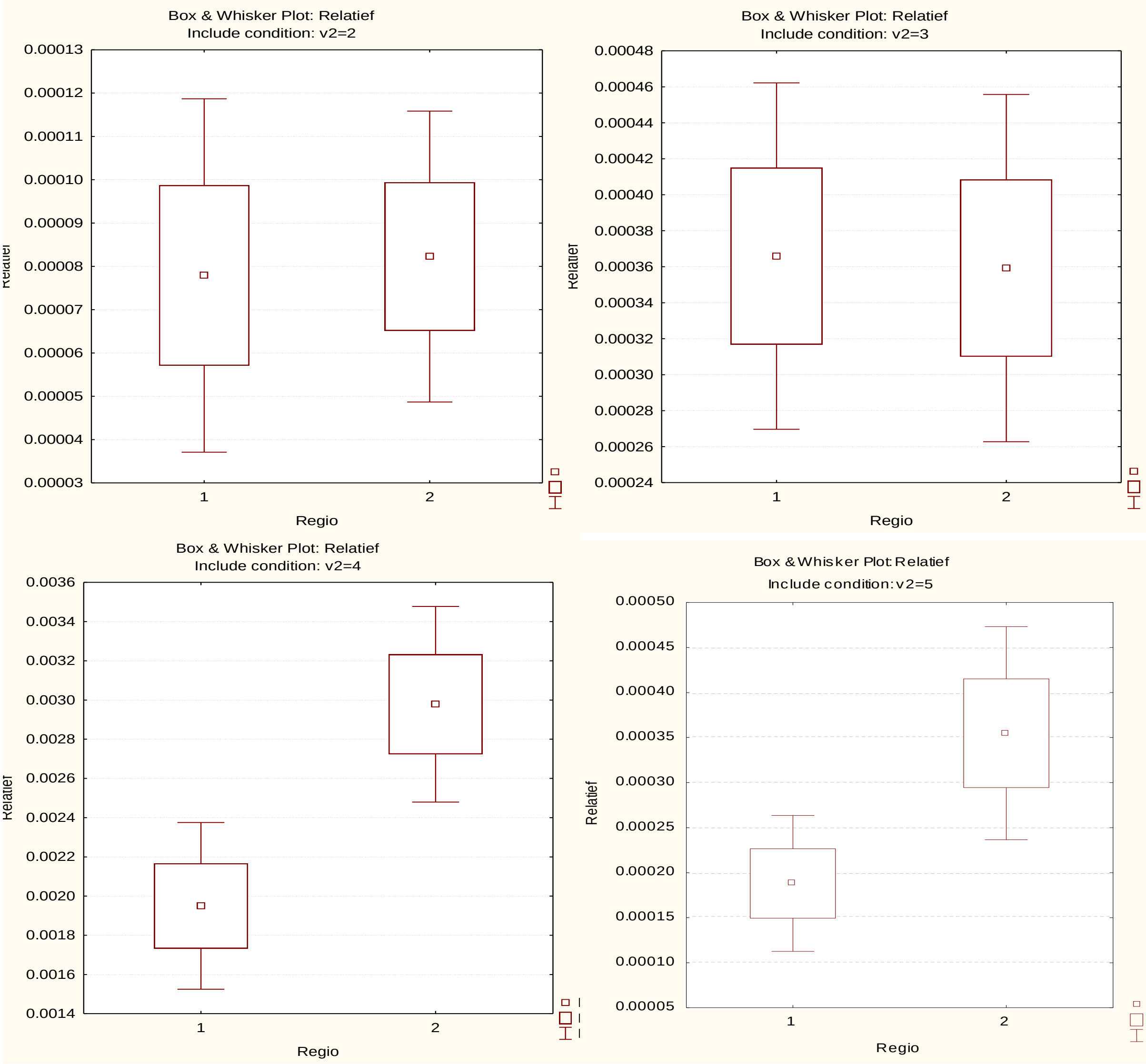
Appendix C. Statistical figures



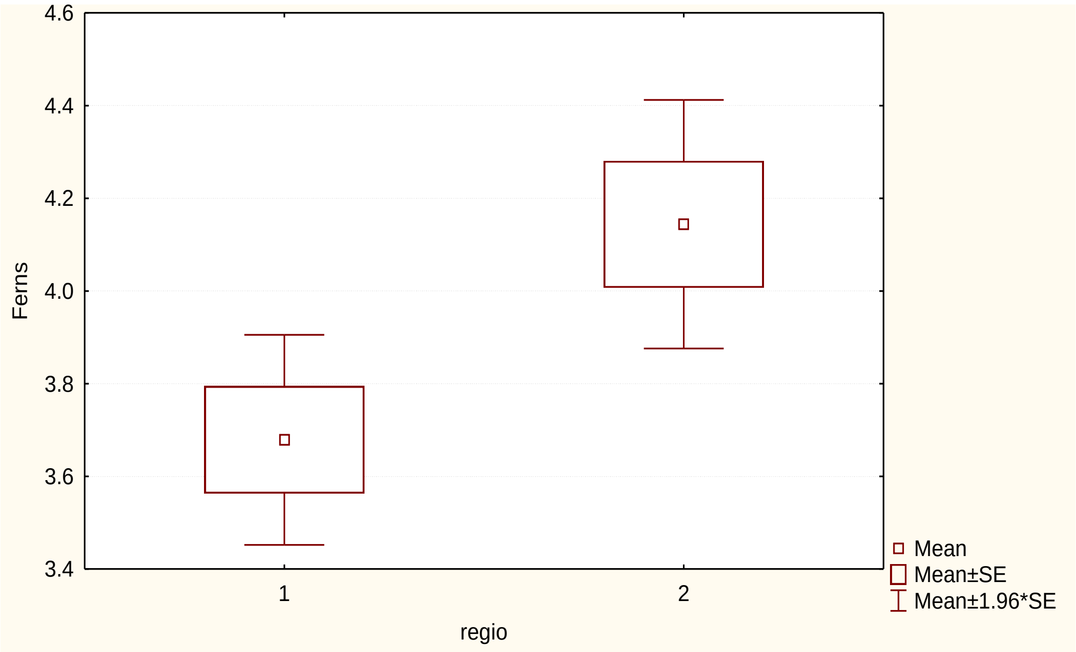
App.C.1: Correlation between CBH of the tree and α-diversity in the tree.



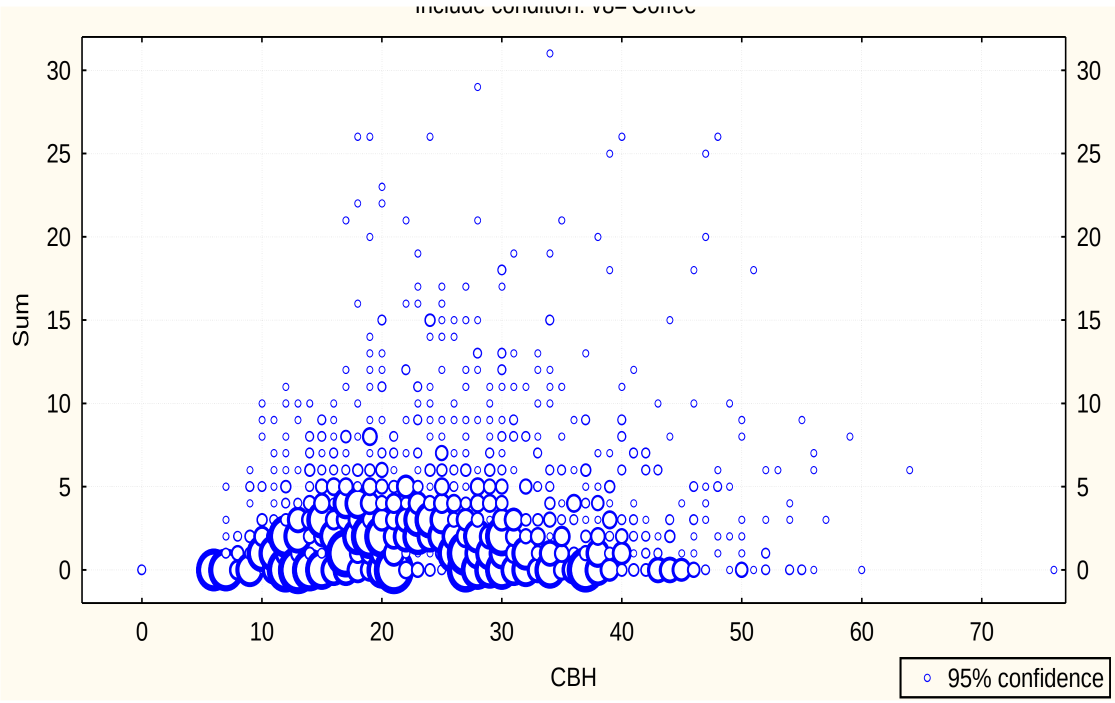
App.C.2: Correlation between the distance of the tree to the forest edge and α-diversity in the tree.



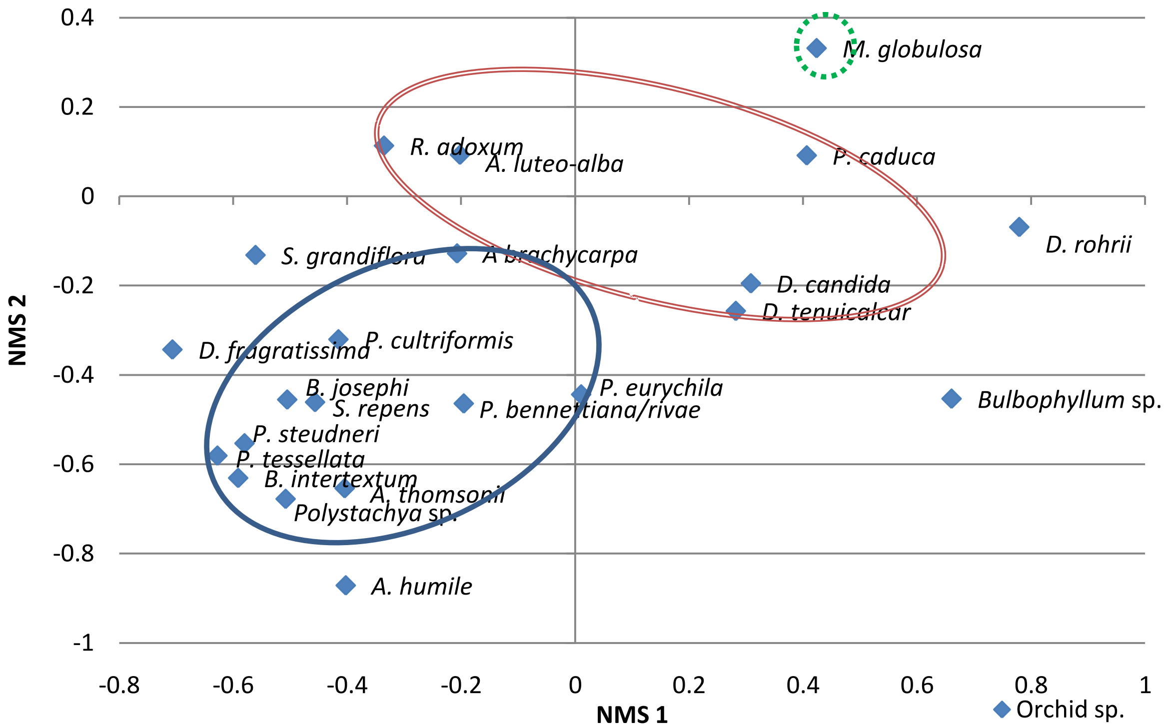
App.C.3: Boxplots of relative abundance of orchids compared between the fragmented forest type (1) and the continuous forest type (2). Upper left; Tree Zone 2, no difference found (p=0.88, t=-0.151), upper right; Tree Zone 3, no difference found (p=0.92, t=0.093), lower left; Tree Zone 4, significant higher relative abundance found in continuous forest type (p=0.002, t=-3.06), lower right; Tree Zone 5, significant higher relative abundance found in continuous forest type (p=0.015, t=-2.443).



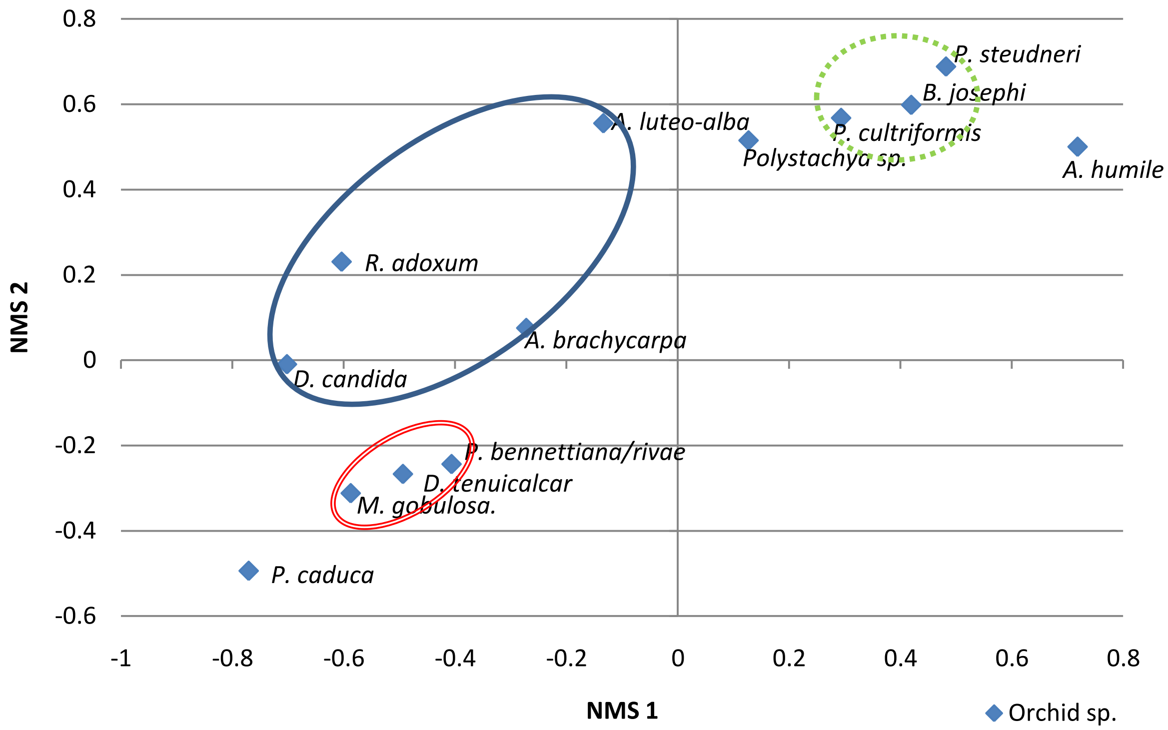
App.C.4: Boxplot of mean α-diversity of ferns, compared between the fragmented forest type (1) and the continuous forest type (2), a significant higher diversity was found for the continuous forest type (p=0.022).



App.C.5: Scatterplot of the CBH of coffee shrubs correlated with the orchid abundance on that shrub (Sum). Highest abundance is found for shrubs with medium CBH. The larger the circle, the more this combination was found in the field.



App.C.6: NMS ordination on species in tree layer. Communities based on Cluster analysis, green speckled circle: sp. indicative for community 3, red dubble circle: spp. indicative for community 1, blue circle: spp. indicative for community 2.



App.C.7: NMS ordination on species in shrub layer. Communities based on Cluster analysis; green speckled circle: spp. indicative for community 3, red dubble circle: spp. indicative for community 1, blue circle: spp. indicative for community 2.