Manuscript Details

Manuscript number	BIOC_2019_472_R1
Title	Rapid diversity and structure degradation over time through continued coffee cultivation in remnant Ethiopian Afromontane forests
Article type	Full Length Article

Abstract

Tropical deforestation and effects on biodiversity and ecosystem services are relatively well studied, but the extent and impact of forest degradation remains much more cryptic. Most of the remaining Ethiopian moist Afromontane forests are currently being degraded due to forest management for coffee production. So far, effects of degradation on biodiversity and forest structure have been estimated by comparing forests with different management regimes in terms of coffee cultivation intensity. Here, we performed an analysis at two time points (2009 and 2017), through the resurveying of 32 plots located in moist Afromontane forest remnants managed for coffee production, to evaluate how rapidly further degradation occurs. In contrast to space-for-time substitutions, our study allows for an accurate assessment of changes in biodiversity and forest structure due to coffee cultivation, without confounding effects of local environmental conditions. We found reductions in woody vegetation richness (-23%) and diversity (-14%), and a further degradation of forest structure, as quantified by tree and shrub density (-31%). Overall tree and shrub height increased over time (+11%). No changes were found in basal area, dominant tree height and woody community composition over an eight-year period. Our findings indicate a continuation in loss of woody vegetation diversity and related ecosystem services due to an intensive low thinning regime where the smallholder coffee farmers removed predominantly intermediate and suppressed trees from the understorey and maintain the tallest trees in the upperstorey. To halt further forest degradation, implementation of REDD+ and coffee certification programs could provide options, however their effectiveness remains to be tested in the field.

Keywords	Coffea arabica; Ecosystem services; Forest management; Forest structure; Species composition; Tropical forest
Taxonomy	Conservation Ecology, Plant Biodiversity, Plant Community Structure, Plant Diversity in Agricultural Landscape, Tropical Forest, Natural Capital
Corresponding Author	Lore Geeraert
Corresponding Author's Institution	University of Leuven (KU Leuven)
Order of Authors	Lore Geeraert, Eva Hulsmans, Kenny Helsen, Gezahegn Berecha, Raf Aerts, Olivier Honnay
Suggested reviewers	Ivette Perfecto, Kristoffer Hylander, Stacy Philpott, Erika Zavaleta

Rapid diversity and structure degradation over time through continued coffee cultivation in remnant Ethiopian Afromontane forests

Abstract

Tropical deforestation and effects on biodiversity and ecosystem services are relatively well studied, but the extent and impact of forest degradation remains much more cryptic. Most of the remaining Ethiopian moist Afromontane forests are currently being degraded due to forest management for coffee production. So far, effects of degradation on biodiversity and forest structure have been estimated by comparing forests with different management regimes in terms of coffee cultivation intensity. Here, we performed an analysis at two time points (2009 and 2017), through the resurveying of 32 plots located in moist Afromontane forest remnants managed for coffee production, to evaluate how rapidly further degradation occurs. In contrast to space-for-time substitutions, our study allows for an accurate assessment of changes in biodiversity and forest structure due to coffee cultivation, without confounding effects of local environmental conditions. We found reductions in woody vegetation richness (-23%) and diversity (-14%), and a further degradation of forest structure, as quantified by tree and shrub density (-31%). Overall tree and shrub height increased over time (+11%). No changes were found in basal area, dominant tree height and woody community composition over an eight-year period. Our findings indicate a continuation in loss of woody vegetation diversity and related ecosystem services due to an intensive low thinning regime where the smallholder coffee farmers removed predominantly intermediate and suppressed trees from the understorey and maintain the tallest trees in the upperstorey. To halt further forest degradation, implementation of REDD+ and coffee certification programs could provide options, however their effectiveness remains to be tested in the field.

Key words

Coffea arabica – Ecosystem services – Forest management – Forest structure – Species composition – Tropical forest

1. Introduction

Natural tropical forests are of global importance in terms of provided ecosystem services and biodiversity, harboring over 50% of the world's species richness (Daily, 1997; Foley et al., 2005; Lewis et al., 2015; UNEP WCMC, 2002). Along with the loss of tropical forest habitat, our world is losing numerous species and important ecosystem services such as global and local climate regulation, carbon sequestration, provisioning of genetic resources (including crop wild relatives and medical resources), and production of food and raw materials (MEA, 2005).

Agricultural expansion is the main driver of tropical deforestation (Curtis et al., 2018; Gibbs et al., 2010; Hosonuma et al., 2012). Across the tropics, agricultural land expanded with more than 100 million ha between 1980 and 2000, of which more than 55% was obtained through deforestation of natural forests (Gibbs et al., 2010). Between 1990 and 2015, ca. 195 million ha of tropical forest cover was cut down (Hansen et al., 2013; Keenan et al., 2015). Nonetheless, the net rates of tropical deforestation are decreasing with time, with an estimated loss of 5.5 million ha year⁻¹ between 2010 and 2015, compared to ca. 9.5 million ha year⁻¹ in the 1990s (Keenan et al., 2015).

While deforestation and its effects on biodiversity and ecosystem services are relatively well studied, the impact of forest degradation has only been acknowledged rather recently (Edwards, 2016). Forest degradation was found to account for ca. 69% of the total carbon losses in the tropics between 2003 and 2014 (Baccini et al., 2017), and for significant biodiversity reductions (Barlow et al., 2016; Gibson et al., 2011; Newbold et al., 2015). Main drivers of human-induced tropical forest degradation include selective logging (Burivalova et al., 2014; Hosonuma et al., 2012), fuelwood collection and charcoal production (Hosonuma et al., 2012), wildfire (Cochrane, 2003; Hosonuma et al., 2012), forest livestock grazing (Hosonuma et al., 2012), and hunting for bush meat (Peres, 2000). In addition, deforestation itself induces degradation of remaining forests due to reduced habitat area, and increased isolation, fragmentation and edge effects (Ewers and Didham, 2005; Ferraz et al., 2007; Haddad et al., 2015). Yet, in contrast to deforestation, the extent and impact of forest degradation is much more challenging to detect and monitor, as many disturbances are more or less concealed by a forest canopy that often remains present (Decuyper et al., 2018; DeVries et al., 2015; Peres et al., 2006). Ongoing debates on the interpretation of forest degradation effects on biodiversity at different spatial scales illustrate this (e.g., Cardinale et al., 2018; Fahrig et al., 2019; Fletcher et al., 2018).

Ethiopia's complex demographic, political, and climatic history has shaped the country's land-use dynamics through time (Reid et al., 2000; Tadesse et al., 2014b; Zewde, 2002). Reported deforestation rates vary, mainly depending on the used definitions of 'forest' in terms of surface area and percentage forest cover, but numbers reach up to ca. 93% forest loss since 1900 (Aleman et al., 2018; Bishaw, 2001; UNEP, 2016; but see McCann, 1997). The forests that remain are predominantly montane forests which are part of the Eastern Afromontane Biodiversity Hotspot, indicating their importance in terms of biodiversity and ecosystem services (Mittermeier et al., 2011). One globally important ecosystem service, provided by intact Ethiopian montane forests, is the supply of genetic resources of wild *Coffea arabica* (Anthony et al., 2002). Whereas various drivers, including agricultural expansion and logging for construction and fuel wood have been linked to deforestation in Ethiopia (Assefa and Bork, 2014; Dessie and Kleman, 2007), the occurrence of wild *C. arabica* has played a significant role in mitigating deforestation rates of Ethiopian moist montane forests (Getahun et al., 2013; Hylander et al., 2013; Tadesse et al., 2014a). The high economic value of Arabica coffee at the world market (ICO, 2018; IMF, 2018) stimulated farmers to conserve parts of these forests for coffee production. As a forest shrub, growing naturally under a dense canopy layer, *C. arabica* depends on shade for optimal growing conditions, hence it has been traditionally cultivated under a relatively dense and species rich canopy cover (Schmitt et al., 2010).

In response to the increasing global coffee demand and human population growth, farmers aim to continuously increase coffee production, at the expense of forest integrity (Decuyper et al., 2018). To boost productivity, farmers increase space and light conditions for the cultivated coffee shrubs. Competing understorey vegetation is removed and trees are selectively cut, systematically taking out the tallest individuals or unwanted species and selecting for preferred shade providing species (Aerts et al., 2011; Schmitt et al., 2010). Reduced shade levels dramatically increase short-term coffee yields, from a mere 15 kg ha⁻¹ in natural forests annually (Schmitt et al., 2010) to 1.7–2.6 metric tonnes ha⁻¹ year⁻¹ in intensively managed systems (Aerts et al., 2011). Preferred shade

providing trees within Ethiopian *C. arabica* production systems are, for example, *Albizia gummifera* and *Albizia schimperiana* which are leguminous trees with a slim trunk and an open, wide-spreading crown, covering an as wide as possible area per trunk (Aerts et al., 2011).

There is increasing evidence of the negative impact of coffee production intensification on the diversity and abundance of forest (specialist) species and on forest structure. Previous studies in Ethiopia have reported a reduced tree and shrub species richness and abundance (Aerts et al., 2011, 2013b; Schmitt et al., 2010; Senbeta and Denich, 2006; Tadesse et al., 2014a), a degraded forest structure (Decuyper et al., 2018), a reduced carbon sequestration capacity (De Beenhouwer et al., 2016), a reduced genetic variation and altered population genetic structure in *C. arabica* (Aerts et al., 2013a; Berecha et al., 2014), and a reduced species richness of epiphytic orchids (De Beenhouwer et al., 2015a; Hundera et al., 2013), specialist forest birds (Gove et al., 2008), insects (Berecha et al., 2015; Geeraert et al., 2018; Jha and Vandermeer, 2010; Samnegård et al., 2014), and mycorrhizal fungi (De Beenhouwer et al., 2015b).

All the above mentioned evidence of negative effects of forest degradation through coffee cultivation is based on chronosequences and associated space-for-time substitution, comparing forests with different management regimes in terms of intensity of coffee cultivation. Even though chronosequences can offer invaluable insights in the ongoing processes (Pickett, 1989; Walker et al., 2010), this indirect approach for measuring temporal dynamics does not provide any information regarding the rate of degradation. In addition, results from space for time substitutions may also partly be caused by differences in local environmental conditions and initial site heterogeneity (Johnson and Miyanishi, 2008; Walker et al., 2010).

Therefore, we compiled a unique dataset of 32 plots (20m × 20m) located in Ethiopian moist Afromontane forest remnants that were surveyed in 2009 and resurveyed in 2017, using standardized methods. This approach allows an accurate quantification of the forest degradation rate caused by forest management for coffee production. We evaluated changes over time in terms of (1) species richness and diversity of woody vegetation and (2) forest structure, as quantified by woody vegetation density, basal area, and overall and dominant tree height.

2. Materials and methods

2.1. Study area

We conducted our research in the highlands of southwestern Ethiopia, in the Mana district (administrative center: Yebu, 7°45'08" N, 36°45'51" E) within the Jimma zone, Oromia region (Fig. 1). The Jimma zone is one of the major Arabica coffee growing zones in Ethiopia. The study landscape was composed of a mosaic of managed coffee forests, annual-crop agricultural land, wood lots for timber production (*Eucalyptus* and *Cupressus*), grazing lands, riverine wetland, and small human settlements. Crops cultivated in the landscape matrix include maize, teff (*Eragrostis tef*), khat (*Catha edulis*), and enset (*Ensete ventricosum*). Ethiopia has a complex forest history (Ameha et al., 2014; McCann, 1997), and due to the lack of historical information it is difficult to know the exact forest cover dynamics within our particular study area. Therefore, it might be possible that at some point in history the original forest cover in our study area already has been subjected to, and recovered from, severe human disturbances. In 2009, local elders stated that the forest was relatively intact ca. 70 years ago, with few coffee shrubs and only sparse human settlement. During both survey years, we noticed remnant canopy trees that are characteristic of natural moist Afromontane forests (e.g., *Pouteria adolfi-friedericii*, *Prunus africanus*, *Schefflera abyssinica*), within and in between the forest fragments of the study area, indicating the former presence of a larger and less disturbed moist Afromontane forest (Aerts et al., 2011). After the recognition of coffee's economic importance and its role in sustaining local livelihood, ca. 70 years ago, farmers started to manage the forest to improve coffee productivity (G. Berecha, 2017, personal observation). The soils are Nitisols. Average annual temperatures are 26 °C during daytime and 13 °C at night. Average annual rainfall is 2008 mm.

The studied forest fragments were all managed by local small-holder farmers for coffee production, and were already in the process of degradation in terms of species composition and forest structure during the first survey in 2009 (Aerts et al., 2011). Management included pruning and stumping of the coffee shrubs, removal of epiphytes that grow on the stem and branches, replacing old

or dead shrubs by locally cultivated coffee seedlings, and slashing the understorey seedlings and weeds once or twice per year. A slight variation in intensity of pruning the coffee shrubs and clearing the understorey was visible, across forests, depending on availability of labor and on experience and knowledge of the farmers about enhancing coffee productivity.

2.2. Study design

A total of 32 forest inventory plots (20×20 m) were surveyed within 24 Afromontane forest fragments that were managed for coffee production (Fig. 1). Forest fragment shapes were digitized and surface areas were calculated in QGIS (QGIS Development Team, 2015). The fragments' surface areas ranged from 0.2 to 93.0 ha (median: 2.1 ha, IQR: 6.8 ha). The plots were established and surveyed for a first time in August 2009 for a study that compared differences in woody species composition, forest structure, and regeneration potential among forests with different management regimes in terms of coffee cultivation intensity (Aerts et al., 2013b). In August 2017, we resurveyed the plots using standardized methods. The original plots were aligned on the Ethiopian national grid (UTM 37N on Adindan datum) with plot boundaries following north-south and east-west orientations. The plots were relocated by use of GPS coordinates (Oregon 700 Garmin) of the southwestern corner of each plot. From this point, we reconstructed the plot toward the north and east by use of compass and measuring tape. Within each plot, abundance and height of all tree and shrub species with a diameter at breast height (DBH) ≥ 5 cm were measured, *C. arabica* shrubs not included. Tree and shrub heights were measured according to the 'angle-measure method' (also called the 'tangent method') (Korning and Thomsen, 1994) with a mechanical clinometer to measure the angles, and a measuring tape to measure the horizontal distance between the observer and the base of the tree. The observer was careful to make a good estimation of the tree top, by standing at a distance as far as possible from the tree. For flat topped trees, the clinometer was aimed at the central point of the upper canopy and not at the edge to avoid overestimation of tree height. Species were identified by local specialists and with the help of literature by Dharani (2002) and Fichtl and Admasu (1994). *Acacia* (*Vachellia/Senegalialia*¹) and *Albizia* species were identified up to genus level, all other species were identified to species level.

2.3. Data analysis

Woody vegetation diversity and forest structure were assessed in 32 plots in 2009 and 2017. We evaluated differences between both years, based on following response variables: Hill's N_0 (i.e., species richness), Hill's N_1 (i.e., exponential of Shannon entropy), Hill's N_2 (i.e., inverse Simpson concentration), woody vegetation density, basal area, and overall and dominant tree height. Hill's N_0 and tree height were directly measured in the field. Hill's N_1 and Hill's N_2 were calculated based on the species abundance data (Chao et al., 2014), using the '*ChaoShannon*' and '*Chaosimpson*' functions, respectively, of the iNEXT package (Hsieh et al., 2016) in R (R Core Team, 2018). Tree and shrub density per hectare was calculated based on the measured abundance on plot level (400 m^2). Basal area (m^2/ha) was calculated based on the DBH of the measured trees and shrubs per plot. Dominant tree height is defined as the average height of the five tallest trees in the plot.

To evaluate differences in woody vegetation and forest structure between both survey years, we applied generalized linear mixed models. We included 'year' (i.e., 2009 or 2017) as a fixed factor, and 'fragment size' (i.e., surface area in ha, continuous variable) as a covariate in the models. We also included the 'year $\times$ fragment size' interaction to evaluate potential differential time effects for fragments of different surface areas. As plots were clustered in 24 forest fragments, we included fragment identity as a random factor in the models to account for pseudo-replication in statistical analyses. Furthermore, we also included plot ID as a random intercept to take into account the repeated measures design (paired data). The models took following form:

response variable $\sim$ *year* + *fragment size* + *year* $\times$ *fragment size* + (1 | *fragment*) + (1 | *plot*).

The response variables Hill's N_0 and tree density comprised discrete, positive, right skewed data. Consequently, we modelled Hill's N_0 using the Poisson probability distribution and a log link function, which is considered the most appropriate distribution for this type of data in the absence of

¹ African *Acacia* species with spinescent stipules (thorns) have been regrouped in the new genus *Vachellia* and those without thorns in *Senegalialia* as the genus name *Acacia* is now reserved for species indigenous to Australia (Dyer, 2014). For the sake of clarity we have maintained the former genus name *Acacia*.

overdispersion (overdispersion: $\chi^2 = 28.88$, $p = 0.999$). Tree density, on the other hand, was modelled using a negative binomial probability distribution with log link function, due to significant overdispersion ($\chi^2 = 332.76$, $p < 0.001$). The other response variables (i.e., Hill's N_1 , Hill's N_2 , basal area, and overall and dominant tree height) comprised positive, continuous, right skewed data. Therefore, these variables were modelled using the Gamma probability distribution with inverse link function. We reduced each full model through backward stepwise model selection based on ΔAIC , and calculated estimated marginal means (EMMs) for each response variable, for each survey year.

We tested for differences in community composition between the two survey years by performing canonical redundancy analysis (RDA). First, we removed the variation attributed to the specific plot using the 'Condition' statement in the RDA model, and then we explicitly tested for the variable 'year' (i.e., 2009 or 2017). We tested for significance based on 1000 permutations. As 2009 and 2017 survey years were paired within each survey plot, we restricted permutations of samples within plots. We, furthermore, visualized potential vegetation changes of the tree and shrub community composition in both time points and across all plots, using a non-metric multidimensional scaling (NMDS) ordination with Bray-Curtis distances on the tree and shrub community composition (*plot* $\times$ *species abundance* matrix). A three-axis solution provided a stress level (0.13) below the threshold (0.20).

We performed all analyses in R, version 3.5.1 (R Core Team, 2018). Poisson and Gamma-distributed models were performed using the 'glmer' function in the lme4 package (Bates et al., 2015). To model the negative binomial probability distribution, we used 'glmmTMB', glmmTMB package (Brooks et al., 2017). Estimated marginal means were calculated using 'emmeans', emmeans package (Lenth, 2018). We used the vegan package (Oksanen et al., 2018) to perform the RDA ('rda'), permutation test ('anova.cca'), and NMDS ordination ('metaMDS'). The 'how' function, vegan package, was used to restrict permutations of samples only within plots ('blocks' = plot). Figures were made using the ggplot2 package (Wickham, 2016).

3. Results

3.1. Woody vegetation diversity and forest structure

A total of 263 trees and shrubs (DBH ≥ 5 cm) and 29 different species, was recorded in 2009, and a total of 181 trees and shrubs belonging to 20 species was recorded in 2017 (Fig. S1, Table S1). For both stem number and number of species, this is equivalent to a reduction of 31% over eight years. Hill's N_0 was reduced by 23% ($\chi^2 = 3.47$, $p = 0.063$), and both Hill's N_1 and Hill's N_2 were reduced by 14% ($\chi^2 = 13.22$, $p < 0.001$; $\chi^2 = 16.04$, $p < 0.001$, respectively; Fig. 2A, Table 1). The forest structure differed between 2009 and 2017 with respect to woody vegetation density, and overall tree and shrub height (Fig. 2B,D; Table 1). Density reduced over time by 31% ($z = -3.39$, $p < 0.001$). Overall tree and shrub height increased over time with 11% ($\chi^2 = 6.79$, $p = 0.009$). No significant changes were found for basal area ($\chi^2 = 0.03$, $p = 0.866$) and dominant tree height ($\chi^2 = 0.93$, $p = 0.761$; Fig. 2C,D; Table 1). Full and reduced models are reported in Tables S4 and S5, respectively.

3.2. Community composition

The dominant woody species in both survey years were *Albizia* spp. (34% and 40% of the total observed abundance in 2009 and 2017, respectively), *Croton macrostachyus* (16% in 2009; 23% in 2017) and *Millettia ferruginea* (10% in 2009; 7% in 2017; Table S1). Group separation based on survey year was not significant following the RDA analysis ($F_{1,31} = 0.96$, $p = 0.410$). NMDS ordination of the 2009 and 2017 woody community compositions showed a large overlap rather than two distinct clusters (Fig. 3A, Fig. S3). A small shift of the confidence ellipses for both years is visible towards the upper right corner of the ordination plot. This shift corresponds with an increased dominance of *Albizia* species over time (Fig. 3B; Fig. S2B; Table S2,S3).

4. Discussion

4.1. Rapid progress of Afromontane forest degradation

Although the studied Afromontane forest remnants appeared as unchanged between 2009 and 2017 in terms of shape, surface area, or degree of isolation as seen on satellite images (e.g., Google Earth, Fig. S4), our results showed a further degradation of forest structure over an eight-year period. We found a reduction in woody vegetation density, species richness, and diversity, while the overall tree height increased, and the basal area and dominant tree height remained unchanged. These findings seem consistent with a low thinning regime where farmers remove predominantly intermediate and suppressed trees from the understorey (Kraft crown classes 4-5), which would otherwise provide unwanted, additional shading of coffee shrubs.

Similar magnitudes of reductions in woody vegetation density, species richness and diversity have also been reported by studies comparing coffee forests with different management intensities in SW Ethiopia (Aerts et al., 2011, 2013b; De Beenhouwer et al., 2016; Schmitt et al., 2010; Senbeta and Denich, 2006). Yet, to the best of our knowledge, our study is the first to elucidate the degradation rate of moist Afromontane forests that are managed for coffee production, over an eight-year period. Furthermore, in contrast to space-for-time substitutions, our analysis at two time points allows for an accurate assessment of changes in woody vegetation diversity and forest structure due to coffee cultivation, without potential confounding effects of different local environmental conditions such as altitude and rainfall which often co-vary with the geographical location of coffee forests of different management intensity in our study region (De Beenhouwer et al., 2016; Walker et al., 2010).

4.2. Ecosystem effects

Thinning improves light conditions in the understorey, not only for coffee and early-successional tree species but also for annual weeds such as *Bidens* sp. which further entices farmers to slash the understorey on a regular basis. Thinning generally reduces the conditions for the succession of shade-tolerant, late successional species of the moist Afromontane forest. Seedling and sapling density of early-successional tree species such as *Albizia* spp. and *M. ferruginea* usually rapidly increase after thinning, but as these are removed by regular slashing, long term crown cover cannot be guaranteed in these forest fragments (Hundera et al., 2015). Previously, farmers already selected the desired amounts of shade, by managing the original Afromontane forest canopy according to a high thinning regime, where trees from the dominant and codominant height classes (Kraft crown classes 1-2) were removed systematically to favor the preferred shade providing tree species such as *Albizia* spp., *C. macrostachyus*, and *M. ferruginea* (Aerts et al., 2011; Belay et al., 2018; Schmitt et al., 2010). Along with a decreasing tree and shrub density and diversity over time, we also observed a further increase in dominance of *Albizia* spp. and *C. macrostachyus*. This indicates that farmers continued to select for a minimum of shade providing species, with the aim to further increase coffee yield.

As forest degradation is positively related to reduced habitat size and increased edge effects (Ewers and Didham, 2005; Ferraz et al., 2007; Haddad et al., 2015), we expected that temporal changes in woody vegetation diversity and forest structure may be less pronounced within the larger fragments in our study area as compared to the smaller fragments. However, in our study we did not find an effect of the different forest fragment sizes in which the survey plots were located. This indicates that the farmers applied a low thinning in an equal magnitude over the whole landscape. As the remaining tree and shrub species have grown over time, the appearance of new tree or shrub individuals in the 2017 survey can be explained by the fact that these individuals were too small (DBH < 5 cm) to be included in the 2009 survey. However, some of these new occurrences could be an effect of potential relocation errors as relocation of the plots was based on GPS coordinates.

With continued management for coffee production, forest degradation continues and unavoidably affects ecosystem functioning and related services (Edwards, 2016). Earlier studies found significant losses of aboveground C-stocks when comparing intact Ethiopian moist Afromontane forests with managed coffee forests through space-for-time substitutions (De Beenhouwer et al., 2016; Vanderhaegen et al., 2015). It is known that massive losses of carbon occur with the removal of large, old trees (Keith et al., 2009; Sist et al., 2014; Stephenson et al., 2014), which are also known to provide several other important ecosystem services, e.g., maintaining microclimatic conditions, nutrient and water cycling, and biodiversity conservation (Lindenmayer et al., 2014; Lindenmayer and Laurance, 2017). The results of our study suggest a continuation in the Ethiopian moist Afromontane forests' loss of C-storage capacity and woody vegetation diversity under a low thinning regime for coffee cultivation.

4.3. Indirect effects on coffee production

Degraded moist Afromontane coffee forests still maintain a higher vegetation diversity compared to other perennial crop systems (e.g., Khat (*Catha edulis*), Eucalyptus trees) or annual-crop systems (Hylander and Nemomissa, 2008; Jara et al., 2017). By providing islands of tree cover in an otherwise open agricultural landscape, it has been acknowledged that even degraded forest fragments make a valuable contribution to the landscape's biodiversity (Bhagwat et al., 2008; Muñoz et al., 2013). However, at the forest level, the reduced complexity in forest structure and a reduced woody vegetation diversity are expected to have a negative impact on the fragment's overall biodiversity, including the coffee pollinator community (Berecha et al., 2015; Geeraert et al., 2018; Klein et al., 2002; Samnegård et al., 2014). The negative effects of reduced pollinator diversity on coffee yield have been discussed before, for example, in the context of coffee production systems in Indonesia (Klein et al., 2003) and Central America (Ricketts et al., 2004; Roubik, 2002; Vergara and Badano, 2009).

Even though short-term higher coffee yields may be obtained when shade is reduced, shade has beneficial effects on coffee quality through reduced light conditions (Geromel et al., 2008), reduced mean air temperatures (Bertrand et al., 2012; Joët et al., 2010), increased relative soil humidity (De Beenhouwer et al., 2015b), and a lower degree of soil erosion and nutrient leaching (Babbar and Zak, 1994). Previous research in SW Ethiopia showed an impoverishment of organoleptic quality of *C. arabica* beans with increasing forest management intensity (Geeraert et al., 2019). Also long-term yield stability benefits from shade through the reduction of alternate bearing and risk of over-bearing (Vaast et al., 2006).

4.4. Implications for conservation

The rapid forest degradation progress found in our study, in already strongly managed forest remnants, suggests that Afromontane forest remnants with less intensified management may suffer from even higher degradation rates since their coffee yield could be increased more easily through reduction of shade levels. Therefore, our study emphasizes the need for conservation of the remaining moist Afromontane forests and their valuable biodiversity and ecosystem services, such as the provisioning of Arabica coffee's genetic resources.

To halt further forest degradation through coffee cultivation, implementation of REDD+ (Reducing Emissions from Deforestation and Forest Degradation, plus the conservation, sustainable management and enhancement of forest carbon stocks) and related policy frameworks could be an option. These frameworks are designed to reduce atmospheric CO₂ emissions from deforestation and forest degradation, and may also result in co-benefits for biodiversity and other ecosystem services (Imai et al., 2014; Sullivan et al., 2017; Venter, 2014). Furthermore, several coffee certification programs aim to compensate farmers for loss of income when forest management is reduced in favor of the local biodiversity (Mitiku et al., 2018). However, premium coffee prices do often not sufficiently compensate for the related yield losses (Mitiku et al., 2017; Perfecto et al., 2005; Vanderhaegen et al., 2018), and in the unique case of Ethiopia, where coffee is a natural understorey species, coffee certification programs may actually be an incentive to convert natural forests into strongly managed yet certified coffee forests (Gove et al., 2008; Hylander et al., 2013).

Under a continued low thinning regime of the studied remnant moist Afromontane forest fragments, the species poor canopy is expected to be conserved, while smaller trees in the understorey will continue to be removed, resulting in additional diversity losses. Conversion of existing degraded forest remnants to more natural Afromontane forest could be achieved through high thinning (e.g., removing some *Albizia* trees from the upper canopy), which would allow other light-demanding species to reach the upper canopy. Reduced slashing, would be another option, allowing shade-demanding species to recruit into the upper canopy, if mature mother trees of such species are still present in, or near, the degraded forest fragments. A number of indigenous tree species (e.g., *Allophylus abyssinicus*, *Ekebergia capensis*, *Prunus africana* and *Syzygium guineense*) provides important ecosystem services such as food, medicine and bee forage in addition to shade for coffee (Teketay et al., 2010). Assisting regeneration of such multipurpose tree species through fencing, seeding or planting of seedlings is also a viable option to restore moist Afromontane forest (Hundera

et al., 2015). Nevertheless, the willingness of farmers to adopt such forest management practices remains to be evaluated in the field.

5. Reference list

- Aerts, R., Berecha, G., Gijbels, P., Hundera, K., Van Glabeke, S., Vandepitte, K., Muys, B., Roldán-Ruiz, I., Honnay, O., 2013a. Genetic variation and risks of introgression in the wild *Coffea arabica* gene pool in south-western Ethiopian montane rainforests. *Evol. Appl.* 6, 243–252. <https://doi.org/10.1111/j.1752-4571.2012.00285.x>
- Aerts, R., Hundera, K., Berecha, G., Gijbels, P., Baeten, M., Van Mechelen, M., Hermy, M., Muys, B., Honnay, O., 2011. Semi-forest coffee cultivation and the conservation of Ethiopian Afromontane rainforest fragments. *For. Ecol. Manage.* 261, 1034–1041. <https://doi.org/10.1016/j.foreco.2010.12.025>
- Aerts, R., Hundera, K., Fontaine, A., Van Mechelen, M., Gijbels, P., Honnay, O., Muys, B., 2013b. Effects of coffee management intensity on composition, structure, and regeneration status of Ethiopian moist evergreen afromontane forests. *Environ. Manage.* 51, 801–809. <https://doi.org/10.1007/s00267-012-9976-5>
- Aleman, J.C., Jarzyna, M.A., Staver, A.C., 2018. Forest extent and deforestation in tropical Africa since 1900. *Nat. Ecol. Evol.* 2, 26–33. <https://doi.org/10.1038/s41559-017-0406-1>
- Ameha, A., Larsen, H.O., Lemenih, M., 2014. Participatory forest management in Ethiopia: Learning from pilot projects. *Environ. Manage.* 53, 838–854. <https://doi.org/10.1007/s00267-014-0243-9>
- Anthony, F., Combes, M.C., Astorga, C., Bertrand, B., Graziosi, G., Lashermes, P., 2002. The origin of cultivated *Coffea arabica* L. varieties revealed by AFLP and SSR markers. *Theor. Appl. Genet.* 104, 894–900. <https://doi.org/10.1007/s00122-001-0798-8>
- Assefa, E., Bork, H.-R., 2014. Deforestation and forest management in southern Ethiopia: Investigations in the Chenchu and Arbaminch areas. *Environ. Manage.* 53, 284–299. <https://doi.org/10.1007/s00267-013-0182-x>
- Babbar, L.I., Zak, D.R., 1994. Nitrogen cycling in coffee agroecosystems: Net N mineralization and nitrification in the presence and absence of shade trees. *Agric. Ecosyst. Environ.* 48, 107–113. [https://doi.org/10.1016/0167-8809\(94\)90081-7](https://doi.org/10.1016/0167-8809(94)90081-7)
- Baccini, A., Walker, W., Carvalho, L., Farina, M., Sulla-Menashe, D., Houghton, R.A., 2017. Tropical forests are a net carbon source based on aboveground measurements of gain and loss. *Science* (80-.). 358, 230–234. <https://doi.org/10.1126/science.aam5962>
- Barlow, J., Lennox, G.D., Ferreira, J., Berenguer, E., Lees, A.C., Nally, R. Mac, Thomson, J.R., Ferraz, S.F. de B., Louzada, J., Oliveira, V.H.F., Parry, L., Ribeiro de Castro Solar, R., Vieira, I.C.G., Aragão, L.E.O.C., Begotti, R.A., Braga, R.F., Cardoso, T.M., Jr, R.C. de O., Souza Jr, C.M., Moura, N.G., Nunes, S.S., Siqueira, J.V., Pardini, R., Silveira, J.M., Vaz-de-Mello, F.Z., Veiga, R.C.S., Venturieri, A., Gardner, T.A., 2016. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature* 535, 144–147. <https://doi.org/10.1038/nature18326>
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.* 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Belay, B., Zewdie, S., Mekuria, W., Abiyu, A., Amare, D., Woldemariam, T., 2018. Woody species diversity and coffee production in remnant semi-natural dry Afromontane Forest in Zegie Peninsula, Ethiopia. *Agrofor. Syst.* <https://doi.org/10.1007/s10457-018-0285-8>
- Berecha, G., Aerts, R., Muys, B., Honnay, O., 2015. Fragmentation and management of Ethiopian moist evergreen forest drive compositional shifts of insect communities visiting wild Arabica coffee flowers. *Environ. Manage.* 55, 373–382. <https://doi.org/10.1007/s00267-014-0393-9>
- Berecha, G., Aerts, R., Vandepitte, K., Van Glabeke, S., Muys, B., Roldán-Ruiz, I., Honnay, O., 2014. Effects of forest management on mating patterns, pollen flow and intergenerational transfer of genetic diversity in wild Arabica coffee (*Coffea arabica* L.) from Afromontane rainforests. *Biol. J. Linn. Soc.* 112, 76–88. <https://doi.org/10.1111/bij.12274>
- Bertrand, B., Boulanger, R., Dussert, S., Ribeyre, F., Berthiot, L., Descroix, F., Joët, T., 2012.

- Climatic factors directly impact the volatile organic compound fingerprint in green Arabica coffee bean as well as coffee beverage quality. *Food Chem.* 135, 2575–2583. <https://doi.org/10.1016/j.foodchem.2012.06.060>
- Bhagwat, S.A., Willis, K.J., Birks, H.J.B., Whittaker, R.J., 2008. Agroforestry: a refuge for tropical biodiversity? *Trends Ecol. Evol.* 23, 261–267. <https://doi.org/10.1016/j.tree.2008.01.005>
- Bishaw, B., 2001. Deforestation and land degradation in the Ethiopian highlands: A strategy for physical recovery. *Northeast Afr. Stud.* 8, 7–25. <https://doi.org/10.1353/nas.2005.0014>
- Brooks, M.E., Kristensen, K., Koen J. van Benthem, A.M., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* 9, 378–400.
- Burivalova, Z., Şekercioğlu, Ç.H., Koh, L.P., 2014. Thresholds of logging intensity to maintain tropical forest biodiversity. *Curr. Biol.* 24, 1893–1898. <https://doi.org/10.1016/j.cub.2014.06.065>
- Cardinale, B.J., Gonzalez, A., Allington, G.R.H., Loreau, M., 2018. Is local biodiversity declining or not? A summary of the debate over analysis of species richness time trends. *Biol. Conserv.* 219, 175–183. <https://doi.org/10.1016/j.biocon.2017.12.021>
- Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., Ellison, A.M., 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecol. Monogr.* 84, 45–67. <https://doi.org/10.1890/13-0133.1>
- Cochrane, M.A., 2003. Fire science for rainforests. *Nature* 421, 913–919. <https://doi.org/10.1038/nature01437>
- Curtis, P.G., Slay, C.M., Harris, N.L., Tyukavina, A., Hansen, M.C., 2018. Classifying drivers of global forest loss. *Science (80-.)*. 361, 1108–1111. <https://doi.org/10.1126/science.aau3445>
- Daily, G.C., 1997. *Nature's services: Societal dependence on natural ecosystems*. Cambridge University Press, Washington, DC.
- De Beenhouwer, M., Aerts, R., Hundera, K., Van Overtveld, K., Honnay, O., 2015a. Management intensification in Ethiopian coffee forests is associated with crown habitat contraction and loss of specialized epiphytic orchid species. *Basic Appl. Ecol.* 16, 592–600. <https://doi.org/10.1016/j.baae.2015.06.006>
- De Beenhouwer, M., Geeraert, L., Mertens, J.E.J., Van Geel, M., Aerts, R., Vanderhaegen, K., Honnay, O., 2016. Biodiversity and carbon storage co-benefits of coffee agroforestry across a gradient of increasing management intensity in the SW Ethiopian highlands. *Agric. Ecosyst. Environ.* 222, 193–199. <https://doi.org/10.1016/j.agee.2016.02.017>
- De Beenhouwer, M., Muleta, D., Peeters, B., Van Geel, M., Lievens, B., Honnay, O., 2015b. DNA pyrosequencing evidence for large diversity differences between natural and managed coffee mycorrhizal fungal communities. *Agron. Sustain. Dev.* 35, 241–249. <https://doi.org/10.1007/s13593-014-0231-8>
- Decuyper, M., Mulatu, K.A., Brede, B., Calders, K., Armston, J., Rozendaal, D.M.A., Mora, B., Clevers, J.G.P.W., Kooistra, L., Herold, M., Bongers, F., 2018. Assessing the structural differences between tropical forest types using Terrestrial Laser Scanning. *For. Ecol. Manage.* 429, 327–335. <https://doi.org/10.1016/j.foreco.2018.07.032>
- Dessie, G., Kleman, J., 2007. Pattern and magnitude of deforestation in the South Central Rift Valley region of Ethiopia. *Mt. Res. Dev.* 27, 162–168. <https://doi.org/10.1659/mrd.0730>
- DeVries, B., Verbesselt, J., Kooistra, L., Herold, M., 2015. Robust monitoring of small-scale forest disturbances in a tropical montane forest using Landsat time series. *Remote Sens. Environ.* 161, 107–121. <https://doi.org/10.1016/j.rse.2015.02.012>
- Dharani, N., 2002. *Guide to common trees and shrubs of East Africa*, 1st ed. Struik Publishers, Cape Town (South Africa).
- Dyer, C., 2014. New names for the African *Acacia* species in *Vachellia* and *Senegalia*. *South. For. a J. For. Sci.* 76, iii–iii. <https://doi.org/10.2989/20702620.2014.980090>
- Edwards, D.P., 2016. The rainforest's “do not disturb” signs. *Nature* 535, 44–45. <https://doi.org/10.1038/nature18901>
- Ewers, R.M., Didham, R.K., 2005. Confounding factors in the detection of species responses to habitat fragmentation. *Biol. Rev.* 81, 117. <https://doi.org/10.1017/S1464793105006949>
- Fahrig, L., Arroyo-Rodríguez, V., Bennett, J.R., Boucher-Lalonde, V., Cazetta, E., Currie, D.J., Eigenbrod, F., Ford, A.T., Harrison, S.P., Jaeger, J.A.G., Koper, N., Martin, A.E., Martin, J.-L.,

- Metzger, J.P., Morrison, P., Rhodes, J.R., Saunders, D.A., Simberloff, D., Smith, A.C., Tischendorf, L., Vellend, M., Watling, J.I., 2019. Is habitat fragmentation bad for biodiversity? *Biol. Conserv.* 230, 179–186. <https://doi.org/10.1016/j.biocon.2018.12.026>
- Ferraz, G., Nichols, J.D., Hines, J.E., Stouffer, P.C., Bierregaard, R.O., Lovejoy, T.E., 2007. A large-scale deforestation experiment: Effects of patch area and isolation on Amazon birds. *Science* (80-.). 315, 238–241. <https://doi.org/10.1126/science.1133097>
- Fichtl, R., Admasu, A., 1994. Honeybee flora of Ethiopia, 1st ed. Margraf Verlag, Weikersheim (Germany).
- Fletcher, R.J., Didham, R.K., Banks-Leite, C., Barlow, J., Ewers, R.M., Rosindell, J., Holt, R.D., Gonzalez, A., Pardini, R., Damschen, E.I., Melo, F.P.L., Ries, L., Prevedello, J.A., Tscharntke, T., Laurance, W.F., Lovejoy, T., Haddad, N.M., 2018. Is habitat fragmentation good for biodiversity? *Biol. Conserv.* 226, 9–15. <https://doi.org/10.1016/j.biocon.2018.07.022>
- Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global consequences of land use. *Science* (80-.). 309, 570–574. <https://doi.org/10.1126/science.1111772>
- Geeraert, L., Aerts, R., Jordaens, K., Dox, I., Wellens, S., Couri, M., Berecha, G., Honnay, O., 2018. Intensification of Ethiopian coffee agroforestry drives impoverishment of the Arabica coffee flower visiting bee and fly communities. *Agrofor. Syst.* <https://doi.org/10.1007/s10457-018-0280-0>
- Geeraert, L., Berecha, G., Honnay, O., Aerts, R., 2019. Organoleptic quality of Ethiopian Arabica coffee deteriorates with increasing intensity of coffee forest management. *J. Environ. Manage.* 231, 282–288. <https://doi.org/10.1016/j.jenvman.2018.10.037>
- Geromel, C., Ferreira, L.P., Davrieux, F., Guyot, B., Ribeyre, F., dos Santos Scholz, M.B., Pereira, L.F.P., Vaast, P., Pot, D., Leroy, T., Filho, A.A., Vieira, L.G.E., Mazzafera, P., Marraccini, P., 2008. Effects of shade on the development and sugar metabolism of coffee (*Coffea arabica* L.) fruits. *Plant Physiol. Biochem.* 46, 569–579. <https://doi.org/10.1016/j.plaphy.2008.02.006>
- Getahun, K., Rompaey, A. Van, Turnhout, P. Van, Poesen, J., 2013. Factors controlling patterns of deforestation in moist evergreen Afromontane forests of Southwest Ethiopia. *For. Ecol. Manage.* 304, 171–181. <https://doi.org/10.1016/j.foreco.2013.05.001>
- Gibbs, H.K., Ruesch, A.S., Achard, F., Clayton, M.K., Holmgren, P., Ramankutty, N., Foley, J.A., 2010. Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. *Proc. Natl. Acad. Sci.* 107, 16732–16737. <https://doi.org/10.1073/pnas.0910275107>
- Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E., Sodhi, N.S., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478, 378–381. <https://doi.org/10.1038/nature10425>
- Gove, A.D., Hylander, K., Nemomisa, S., Shimelis, A., 2008. Ethiopian coffee cultivation - Implications for bird conservation and environmental certification. *Conserv. Lett.* 1, 208–216. <https://doi.org/10.1111/j.1755-263X.2008.00033.x>
- Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.-X., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* 1, 1–9. <https://doi.org/10.1126/sciadv.1500052>
- Hansen, M.C., Potapov, P. V, Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S. V, Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., Townshend, J.R.G., 2013. High-resolution global maps of 21st-century forest cover change. *Science* (80-.). 342, 850–853. <https://doi.org/10.1126/science.1244693>
- Hosonuma, N., Herold, M., De Sy, V., De Fries, R.S., Brockhaus, M., Verchot, L., Angelsen, A., Romijn, E., 2012. An assessment of deforestation and forest degradation drivers in developing countries. *Environ. Res. Lett.* 7, 044009. <https://doi.org/10.1088/1748-9326/7/4/044009>
- Hsieh, T.C., Ma, K.H., Chao, A., 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods Ecol. Evol.* 7, 1451–1456. <https://doi.org/10.1111/2041-210X.12613>

- Hundera, K., Aerts, R., De Beenhouwer, M., Van Overtveld, K., Helsen, K., Muys, B., Honnay, O., 2013. Both forest fragmentation and coffee cultivation negatively affect epiphytic orchid diversity in Ethiopian moist evergreen Afromontane forests. *Biol. Conserv.* 159, 285–291. <https://doi.org/10.1016/j.biocon.2012.10.029>
- Hundera, K., Honnay, O., Aerts, R., Muys, B., 2015. The potential of small exclosures in assisting regeneration of coffee shade trees in South-Western Ethiopian coffee forests. *Afr. J. Ecol.* 53, 389–397. <https://doi.org/10.1111/aje.12203>
- Hylander, K., Nemomissa, S., 2008. Home garden coffee as a repository of epiphyte biodiversity in Ethiopia. *Front. Ecol. Environ.* 6, 524–528. <https://doi.org/10.1890/080001>
- Hylander, K., Nemomissa, S., Delrue, J., Enkosa, W., 2013. Effects of coffee management on deforestation rates and forest integrity. *Conserv. Biol.* 27, 1031–1040. <https://doi.org/10.1111/cobi.12079>
- ICO, 2018. Coffee Market Report: December 2018. International Coffee Organization (Downloaded from <http://www.ico.org/Market-Report-18-19-e.asp>).
- Imai, N., Tanaka, A., Samejima, H., Sugau, J.B., Pereira, J.T., Titin, J., Kurniawan, Y., Kitayama, K., 2014. Tree community composition as an indicator in biodiversity monitoring of REDD+. *For. Ecol. Manage.* 313, 169–179. <https://doi.org/10.1016/j.foreco.2013.10.041>
- IMF, 2018. The Federal Democratic Republic of Ethiopia: IMF country report December 2018. International Monetary Fund country report No. 18/354 (Downloaded from <https://www.imf.org/en/Publications/Search?series=IMF+Staff+Country+Reports&when=During&year=2018&title=E>).
- Jara, T., Hylander, K., Nemomissa, S., 2017. Tree diversity across different tropical agricultural land use types. *Agric. Ecosyst. Environ.* 240, 92–100. <https://doi.org/10.1016/j.agee.2017.01.042>
- Jha, S., Vandermeer, J.H., 2010. Impacts of coffee agroforestry management on tropical bee communities. *Biol. Conserv.* 143, 1423–1431. <https://doi.org/10.1016/j.biocon.2010.03.017>
- Joët, T., Laffargue, A., Descroix, F., Doubeau, S., Bertrand, B., Kochko, A. de, Dussert, S., 2010. Influence of environmental factors, wet processing and their interactions on the biochemical composition of green Arabica coffee beans. *Food Chem.* 118, 693–701. <https://doi.org/10.1016/j.foodchem.2009.05.048>
- Johnson, E.A., Miyanishi, K., 2008. Testing the assumptions of chronosequences in succession. *Ecol. Lett.* 11, 419–431. <https://doi.org/10.1111/j.1461-0248.2008.01173.x>
- Keenan, R.J., Reams, G.A., Achard, F., de Freitas, J. V., Grainger, A., Lindquist, E., 2015. Dynamics of global forest area: Results from the FAO Global Forest Resources Assessment 2015. *For. Ecol. Manage.* 352, 9–20. <https://doi.org/10.1016/j.foreco.2015.06.014>
- Keith, H., Mackey, B.G., Lindenmayer, D.B., 2009. Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. *Proc. Natl. Acad. Sci.* 106, 11635–11640. <https://doi.org/10.1073/pnas.0901970106>
- Klein, A.-M., Steffan-Dewenter, I., Buchori, D., Tscharntke, T., 2002. Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. *Conserv. Biol.* 16, 1003–1014. <https://doi.org/10.1046/j.1523-1739.2002.00499.x>
- Klein, A.-M., Steffan-Dewenter, I., Tscharntke, T., 2003. Fruit set of highland coffee increases with the diversity of pollinating bees. *Proc. Biol. Sci.* 270, 955–61. <https://doi.org/10.1098/rspb.2002.2306>
- Korning, J., Thomsen, K., 1994. A new method for measuring tree height in tropical rain forest. *J. Veg. Sci.* 5, 139–140. <https://doi.org/10.2307/3235647>
- Lenth, R., 2018. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.3.0. (<https://CRAN.R-project.org/package=emmeans>).
- Lewis, S.L., Edwards, D.P., Galbraith, D., 2015. Increasing human dominance of tropical forests. *Science* (80-.). 349, 827–832. <https://doi.org/10.1126/science.aaa9932>
- Lindenmayer, D.B., Laurance, W.F., 2017. The ecology, distribution, conservation and management of large old trees. *Biol. Rev.* 92, 1434–1458. <https://doi.org/10.1111/brev.12290>
- Lindenmayer, D.B., Laurance, W.F., Franklin, J.F., Likens, G.E., Banks, S.C., Blanchard, W., Gibbons, P., Ikin, K., Blair, D., McBurney, L., Manning, A.D., Stein, J.A.R., 2014. New policies for old trees: Averting a global crisis in a keystone ecological structure. *Conserv. Lett.* 7, 61–69. <https://doi.org/10.1111/conl.12013>

- McCann, J.C., 1997. The plow and the forest: Narratives of deforestation in Ethiopia, 1840–1992. *Environ. Hist. Durh. N. C.* 2, 138–159. <https://doi.org/10.2307/3985505>
- MEA, 2005. Ecosystems and human well-being: Synthesis. The Millennium Ecosystem Assessment series. Island Press, Washington, DC.
- Mitiku, F., Mey, Y. de, Nyssen, J., Maertens, M., 2017. Do private sustainability standards contribute to income growth and poverty alleviation? A comparison of different coffee certification schemes in Ethiopia. *Sustain.* 9. <https://doi.org/10.3390/su9020246>
- Mitiku, F., Nyssen, J., Maertens, M., 2018. Certification of semi-forest coffee as a land-sharing strategy in Ethiopia. *Ecol. Econ.* 145, 194–204. <https://doi.org/10.1016/j.ecolecon.2017.09.008>
- Mittermeier, R.A., Turner, W.R., Larsen, F.W., Larsen Wugt, F., 2011. Biodiversity Hotspots. <https://doi.org/10.1007/978-3-642-20992-5>
- Muñoz, J.C., Aerts, R., Thijs, K.W., Stevenson, P.R., Muys, B., Sekercioglu, C.H., 2013. Contribution of woody habitat islands to the conservation of birds and their potential ecosystem services in an extensive Colombian rangeland. *Agric. Ecosyst. Environ.* 173, 13–19. <https://doi.org/10.1016/j.agee.2013.04.006>
- Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhusseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L.P., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G.M., Scharlemann, J.P.W., Purvis, A., 2015. Global effects of land use on local terrestrial biodiversity. *Nature* 520, 45–50. <https://doi.org/10.1038/nature14324>
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2018. *vegan: Community Ecology Package*. R package version 2.5-3. (<https://CRAN.R-project.org/package=vegan>).
- Peres, C.A., 2000. Effects of Subsistence Hunting on Vertebrate Community Structure in Amazonian Forests. *Conserv. Biol.* 14, 240–253. <https://doi.org/10.1046/j.1523-1739.2000.98485.x>
- Peres, C.A., Barlow, J., Laurance, W.F., 2006. Detecting anthropogenic disturbance in tropical forests. *Trends Ecol. Evol.* 21, 227–229. <https://doi.org/10.1016/j.tree.2006.03.007>
- Perfecto, I., Vandermeer, J., Mas, A., Pinto, L.S., 2005. Biodiversity, yield, and shade coffee certification. *Ecol. Econ.* 54, 435–446. <https://doi.org/10.1016/j.ecolecon.2004.10.009>
- Pickett, S.T.A., 1989. Space-for-Time Substitution as an Alternative to Long-Term Studies, in: Likens, G.E. (Ed.), *Long-Term Studies in Ecology*. Springer New York, New York, NY, pp. 110–135. https://doi.org/10.1007/978-1-4615-7358-6_5
- QGIS Development Team, 2015. QGIS Geographic Information System.
- R Core Team, 2018. R: A language and environment for statistical computing.
- Reid, R.S., Kruska, R.L., Muthui, N., Taye, A., Wotton, S., Wilson, C.J., Mulatu, W., 2000. Land-use and land-cover dynamics in response to changes in climatic, biological and socio-political forces: The case of southwestern Ethiopia. *Landsc. Ecol.* 15, 339–355. <https://doi.org/10.1023/A:1008177712995>
- Ricketts, T.H., Daily, G.C., Ehrlich, P.R., Michener, C.D., 2004. Economic value of tropical forest to coffee production. *Proc. Natl. Acad. Sci.* 101, 12579–12582.
- Roubik, D.W., 2002. The value of bees to the coffee harvest. *Nature* 417, 708. [https://doi.org/10.1002/\(SICI\)1097-0177\(199909\)216:1<1::AID-DVDY1>3.0.CO;2-T](https://doi.org/10.1002/(SICI)1097-0177(199909)216:1<1::AID-DVDY1>3.0.CO;2-T)
- Samnegård, U., Hambäck, P.A., Nemomissa, S., Hylander, K., 2014. Dominance of the semi-wild honeybee as coffee pollinator across a gradient of shade-tree structure in Ethiopia. *J. Trop. Ecol.* 30, 401–408. <https://doi.org/10.1017/s0266467414000327>
- Schmitt, C.B., Senbeta, F., Denich, M., Preisinger, H., Boehmer, H.J., 2010. Wild coffee management and plant diversity in the montane rainforest of southwestern Ethiopia. *Afr. J. Ecol.* 48, 78–86. <https://doi.org/10.1111/j.1365-2028.2009.01084.x>
- Senbeta, F., Denich, M., 2006. Effects of wild coffee management on species diversity in the Afromontane rainforests of Ethiopia. *For. Ecol. Manage.* 232, 68–74. <https://doi.org/10.1016/j.foreco.2006.05.064>
- Sist, P., Mazzei, L., Blanc, L., Rutishauser, E., 2014. Large trees as key elements of carbon storage

- and dynamics after selective logging in the Eastern Amazon. *For. Ecol. Manage.* 318, 103–109. <https://doi.org/10.1016/j.foreco.2014.01.005>
- Stephenson, N.L., Das, A.J., Condit, R., Russo, S.E., Baker, P.J., Beckman, N.G., Coomes, D.A., Lines, E.R., Morris, W.K., Rüger, N., Álvarez, E., Blundo, C., Bunyavejchewin, S., Chuyong, G., Davies, S.J., Duque, Á., Ewango, C.N., Flores, O., Franklin, J.F., Grau, H.R., Hao, Z., Harmon, M.E., Hubbell, S.P., Kenfack, D., Lin, Y., Makana, J.-R., Malizia, A., Malizia, L.R., Pabst, R.J., Pongpattananurak, N., Su, S.-H., Sun, I.-F., Tan, S., Thomas, D., van Mantgem, P.J., Wang, X., Wiser, S.K., Zavala, M.A., 2014. Rate of tree carbon accumulation increases continuously with tree size. *Nature* 507, 90–93. <https://doi.org/10.1038/nature12914>
- Sullivan, M.J.P., Talbot, J., Lewis, S.L., Phillips, O.L., Qie, L., Begne, S.K., Chave, J., Cuni-Sanchez, A., Hubau, W., Lopez-Gonzalez, G., Miles, L., Monteagudo-Mendoza, A., Sonké, B., Sunderland, T., ter Steege, H., White, L.J.T., Affum-Baffoe, K., Aiba, S., de Almeida, E.C., de Oliveira, E.A., Alvarez-Loayza, P., Dávila, E.Á., Andrade, A., Aragão, L.E.O.C., Ashton, P., Aymard, C., G.A., Baker, T.R., Balinga, M., Banin, L.F., Baraloto, C., Bastin, J.-F., Berry, N., Bogaert, J., Bonal, D., Bongers, F., Brien, R., Camargo, J.L.C., Cerón, C., Moscoso, V.C., Chezeaux, E., Clark, C.J., Pacheco, Á.C., Comiskey, J.A., Valverde, F.C., Coronado, E.N.H., Dargie, G., Davies, S.J., De Canniere, C., Djuikouo, K., M.N., Doucet, J.-L., Erwin, T.L., Espejo, J.S., Ewango, C.E.N., Fauset, S., Feldpausch, T.R., Herrera, R., Gilpin, M., Gloor, E., Hall, J.S., Harris, D.J., Hart, T.B., Kartawinata, K., Kho, L.K., Kitayama, K., Laurance, S.G.W., Laurance, W.F., Leal, M.E., Lovejoy, T., Lovett, J.C., Lukas, F.M., Makana, J.-R., Malhi, Y., Maracahipes, L., Marimon, B.S., Junior, B.H.M., Marshall, A.R., Morandi, P.S., Mukendi, J.T., Mukinzi, J., Nilus, R., Vargas, P.N., Camacho, N.C.P., Pardo, G., Peña-Claros, M., Pétronelli, P., Pickavance, G.C., Poulsen, A.D., Poulsen, J.R., Primack, R.B., Priyadi, H., Quesada, C.A., Reitsma, J., Réjou-Méchain, M., Restrepo, Z., Rutishauser, E., Salim, K.A., Salomão, R.P., Samsodin, I., Sheil, D., Sierra, R., Silveira, M., Slik, J.W.F., Steel, L., Taedoumg, H., Tan, S., Terborgh, J.W., Thomas, S.C., Toledo, M., Umunay, P.M., Gamarra, L.V., Vieira, I.C.G., Vos, V.A., Wang, O., Willcock, S., Zemagho, L., 2017. Diversity and carbon storage across the tropical forest biome. *Sci. Rep.* 7, 39102. <https://doi.org/10.1038/srep39102>
- Tadesse, G., Zavaleta, E., Shennan, C., 2014a. Coffee landscapes as refugia for native woody biodiversity as forest loss continues in southwest Ethiopia. *Biol. Conserv.* 169, 384–391. <https://doi.org/10.1016/j.biocon.2013.11.034>
- Tadesse, G., Zavaleta, E., Shennan, C., FitzSimmons, M., 2014b. Policy and demographic factors shape deforestation patterns and socio-ecological processes in southwest Ethiopian coffee agroecosystems. *Appl. Geogr.* 54, 149–159. <https://doi.org/10.1016/j.apgeog.2014.08.001>
- Teketay, D., Senbeta, F., Maclachlan, M., Bekele, M., Barklund, P., 2010. Edible wild plants in Ethiopia. Addis Ababa University Press, Addis Ababa.
- UNEP, 2016. The contribution of forests to national income in Ethiopia and linkages with REDD+. United Nations Environment Programme (UNEP), United Nations Environment Programme. Nairobi (Kenya).
- UNEP WCMC, 2002. World atlas of biodiversity: Earth's living resources in the 21st century. Prepared by the United Nations Environment Programme (UNEP) World Conservation Monitoring Centre (WCMC). University of California Press, Berkeley (USA).
- Vaast, P., Bertrand, B., Perriot, J.J., Guyot, B., Génard, M., 2006. Fruit thinning and shade improve bean characteristics and beverage quality of coffee (*Coffea arabica* L.) under optimal conditions. *J. Sci. Food Agric.* 86, 197–204. <https://doi.org/10.1002/jsfa.2338>
- Vanderhaegen, K., Teopista, K., Dekoninck, W., Jocqué, R., Muys, B., 2018. Do private coffee standards 'walk the talk' in improving socio-economic and environmental sustainability? *Glob. Environ. Chang.* 51, 1–9. <https://doi.org/10.1016/j.gloenvcha.2018.04.014>
- Vanderhaegen, K., Verbist, B., Hundera, K., Muys, B., 2015. REALU vs. REDD+: Carbon and biodiversity in the Afromontane landscapes of SW Ethiopia. *For. Ecol. Manage.* 343, 22–33. <https://doi.org/10.1016/j.foreco.2015.01.016>
- Venter, O., 2014. Corridors of carbon and biodiversity. *Nat. Clim. Chang.* 4, 91–92. <https://doi.org/10.1038/nclimate2115>
- Vergara, C.H., Badano, E.I., 2009. Pollinator diversity increases fruit production in Mexican coffee plantations: The importance of rustic management systems. *Agric. Ecosyst. Environ.* 129, 117–

687 123. <https://doi.org/10.1016/j.agee.2008.08.001>
688 Walker, L.R., Wardle, D.A., Bardgett, R.D., Clarkson, B.D., 2010. The use of chronosequences in
689 studies of ecological succession and soil development. *J. Ecol.* 98, 725–736.
690 <https://doi.org/10.1111/j.1365-2745.2010.01664.x>
691 Wickham, H., 2016. *ggplot2: Elegant graphics for data analysis*, 2nd ed. Springer-Verlag, New York.
692 Zewde, B., 2002. *A history of modern Ethiopia 1855-1991*, 2nd ed. Addis Ababa University Printing
693 Press.
694
695

Figure. 1. Location of the 32 study plots in selected moist Afromontane forest fragments in Mana district, situated between the towns of Jimma and Agaro (Jimma zone, Oromia region, Southwest-Ethiopia). Dotted lines represent asphalt road.

Figure 2. Estimated marginal means comparing forest diversity and structure in 32 plots within moist Afromontane forest remnants in 2009 and 2017. **(A)** Hill's N_0 , Hill's N_1 , and Hill's N_2 in effective number of tree and shrub species; **(B)** Density in number of trees and shrubs ha^{-1} ; **(C)** Basal area in $\text{m}^2 \text{ha}^{-1}$; **(D)** Overall and dominant tree height in m. Boxes represent the 95% confidence interval, horizontal lines within the boxes represent EMM values. Codes for significant differences between the two years: $\cdot p = 0.1 - 0.05$, $* p = 0.05 - 0.01$, $** p = 0.01 - 0.001$, $*** p \leq 0.001$

Figure 3. Non-metric multidimensional scaling (NMDS) ordination of 32 plots surveyed in 2009 (●) and the same 32 plots surveyed in 2017 (▲). The ordination shows the vegetation species community composition for both survey years, plots located close to each other share a similar community composition of woody species (DBH ≥ 5 cm). Size of the plotted symbols correspond with surface area (ha) of the forest fragment in which the plots were located. (A) Confidence ellipses based on the standard deviations of the points for both survey years are presented. The symbols of certain plots overlap, therefore all plots are individually indicated in Fig. S2A. (B) Indication of woody species in the ordination. The shift in community composition per plot between survey years is visualized in Fig. S2C, and species names are listed in Table S1. NMDS ordinations of the third axis are presented in Fig. S3.

Table 1. Estimated marginal means (EMM) and standard errors (SE), differences between both years (Δ), test statistics, and p -values summarized for the evaluated forest diversity and structure elements.

	2009 (n = 32) EMM ($\pm$ SE)	2017 (n = 32) EMM ($\pm$ SE)	Δ (%)	Test statistic	p
<i>Woody vegetation diversity</i>					
Hill's N_0	3.30 ($\pm$ 0.37)	2.53 ($\pm$ 0.32)	-0.77 (-23.4%)	$\chi^2 = 3.47$	0.063
Hill's N_1	1.85 ($\pm$ 0.25)	1.59 ($\pm$ 0.19)	-0.26 (-14.1%)	$\chi^2 = 13.22$	< 0.001
Hill's N_2	1.67 ($\pm$ 0.21)	1.44 ($\pm$ 0.16)	-0.23 (-13.8%)	$\chi^2 = 16.04$	< 0.001
<i>Forest structure</i>					
Basal area	18.53 ($\pm$ 2.46)	18.14 ($\pm$ 2.39)	-0.39 (-2.1%)	$\chi^2 = 0.03$	0.866
Density	191.84 ($\pm$ 19.09)	132.72 ($\pm$ 13.30)	-59.12 (-30.8%)	$z = -3.39$	< 0.001
Tree height	10.99 ($\pm$ 0.68)	12.22 ($\pm$ 0.83)	1.23 (+11.2%)	$\chi^2 = 6.79$	0.009
Dominant tree height	13.81 ($\pm$ 0.83)	13.66 ($\pm$ 0.81)	-0.15 (-1.1%)	$\chi^2 = 0.93$	0.761

Rapid diversity and structure degradation over time through continued coffee cultivation in remnant Ethiopian Afromontane forests

Highlights

- Afromontane forest degradation quantification through analysis at two time points
- Coffee cultivation degrades Ethiopian moist Afromontane forests over time
- Forest degradation continues in already strongly managed coffee forest remnants
- Low thinning regime negatively affects vegetation diversity and forest structure

Rapid diversity and structure degradation over time through continued coffee cultivation in remnant Ethiopian Afromontane forests

L. Geeraert^{a†*}, E. Hulsmans^{a†}, K. Helsen^a, G. Berecha^b, R. Aerts^{a,c}, O. Honnay^a

^a Plant Conservation and Population Biology, University of Leuven, Kasteelpark Arenberg 31, box 2435, BE-3001 Leuven, Belgium. *lore.geeraert@kuleuven.be*; *eva.hulsmans@kuleuven.be*; *kenny.helsen@kuleuven.be*; *raf.aerts@kuleuven.be*; *olivier.honnay@kuleuven.be*

^b Department of Horticulture and Plant Science, Jimma University, P.O. Box 378, Jimma, Ethiopia. *gberecha@yahoo.com*

^c Division Forest, Nature and Landscape, University of Leuven, Celestijnenlaan 200E, box 2411, BE-3001 Leuven, Belgium. *raf.aerts@kuleuven.be*

* Corresponding author: *lore.geeraert@kuleuven.be* ; +3216320375

† These authors contributed equally.

Acknowledgements

We gratefully acknowledge all farmers who allowed us to work in their coffee forests, and Daniel Damtew (research assistant at Jimma University) for his profound assistance during data collection.

Authors' contributions

EH, LG, RA, OH and GB conceived the idea and designed the study. EH and LG performed the field work. LG, KH, and EH performed the statistical analyses, which were verified by RA and OH. OH, RA and GB supervised the development of the work. All authors contributed to the interpretation of the results and to preparing, discussing, and editing the manuscript, and LG led the writing of the manuscript. All authors gave final approval for publication and have no competing interests and no conflict of interest. All appropriate ethics and other approvals were obtained for the research. No direct financial benefits towards the authors will result from publication of this work.

Funding: This work was financially supported by the Flemish Interuniversity Council (VLIR-UOS).

Rapid diversity and structure degradation over time through continued coffee cultivation in remnant Ethiopian Afromontane forests

Abstract

Tropical deforestation and effects on biodiversity and ecosystem services are relatively well studied, but the extent and impact of forest degradation remains much more cryptic. Most of the remaining Ethiopian moist Afromontane forests are currently being degraded due to forest management for coffee production. So far, effects of degradation on biodiversity and forest structure have been estimated by comparing forests with different management regimes in terms of coffee cultivation intensity. Here, we performed an analysis at two time points (2009 and 2017), through the resurveying of 32 plots located in moist Afromontane forest remnants managed for coffee production, to evaluate how rapidly further degradation occurs. In contrast to space-for-time substitutions, our study allows for an accurate assessment of changes in biodiversity and forest structure due to coffee cultivation, without confounding effects of local environmental conditions. We found reductions in woody vegetation richness (-23%) and diversity (-14%), and a further degradation of forest structure, as quantified by tree and shrub density (-31%). Overall tree and shrub height increased over time (+11%). No changes were found in basal area, dominant tree height and woody community composition over an eight-year period. Our findings indicate a continuation in loss of woody vegetation diversity and related ecosystem services due to an intensive low thinning regime where the smallholder coffee farmers removed predominantly intermediate and suppressed trees from the understorey and maintain the tallest trees in the upperstorey. To halt further forest degradation, implementation of REDD+ and coffee certification programs could provide options, however their effectiveness remains to be tested in the field.

Key words

Coffea arabica – Ecosystem services – Forest management – Forest structure – Species composition – Tropical forest

1. Introduction

Natural tropical forests are of global importance in terms of provided ecosystem services and biodiversity, harboring over 50% of the world's species richness (Daily, 1997; Foley et al., 2005; Lewis et al., 2015; UNEP WCMC, 2002). Along with the loss of tropical forest habitat, our world is losing numerous species and important ecosystem services such as global and local climate regulation, carbon sequestration, provisioning of genetic resources (including crop wild relatives and medical resources), and production of food and raw materials (MEA, 2005).

Agricultural expansion is the main driver of tropical deforestation (Curtis et al., 2018; Gibbs et al., 2010; Hosonuma et al., 2012). Across the tropics, agricultural land expanded with more than 100 million ha between 1980 and 2000, of which more than 55% was obtained through deforestation of natural forests (Gibbs et al., 2010). Between 1990 and 2015, ca. 195 million ha of tropical forest cover was cut down (Hansen et al., 2013; Keenan et al., 2015). Nonetheless, the net rates of tropical deforestation are decreasing with time, with an estimated loss of 5.5 million ha year⁻¹ between 2010 and 2015, compared to ca. 9.5 million ha year⁻¹ in the 1990s (Keenan et al., 2015).

While deforestation and its effects on biodiversity and ecosystem services are relatively well studied, the impact of forest degradation has only been acknowledged rather recently (Edwards, 2016). Forest degradation was found to account for ca. 69% of the total carbon losses in the tropics between 2003 and 2014 (Baccini et al., 2017), and for significant biodiversity reductions (Barlow et al., 2016; Gibson et al., 2011; Newbold et al., 2015). Main drivers of human-induced tropical forest degradation include selective logging (Burivalova et al., 2014; Hosonuma et al., 2012), fuelwood collection and charcoal production (Hosonuma et al., 2012), wildfire (Cochrane, 2003; Hosonuma et al., 2012), forest livestock grazing (Hosonuma et al., 2012), and hunting for bush meat (Peres, 2000). In addition, deforestation itself induces degradation of remaining forests due to reduced habitat area, and increased isolation, fragmentation and edge effects (Ewers and Didham, 2005; Ferraz et al., 2007; Haddad et al., 2015). Yet, in contrast to deforestation, the extent and impact of forest degradation is much more challenging to detect and monitor, as many disturbances are more or less concealed by a forest canopy that often remains present (Decuyper et al., 2018; DeVries et al., 2015; Peres et al., 2006). Ongoing debates on the interpretation of forest degradation effects on biodiversity at different spatial scales illustrate this (e.g., Cardinale et al., 2018; Fahrig et al., 2019; Fletcher et al., 2018).

Ethiopia's complex demographic, political, and climatic history has shaped the country's land-use dynamics through time (Reid et al., 2000; Tadesse et al., 2014b; Zewde, 2002). Reported deforestation rates vary, mainly depending on the used definitions of 'forest' in terms of surface area and percentage forest cover, but numbers reach up to ca. 93% forest loss since 1900 (Aleman et al., 2018; Bishaw, 2001; UNEP, 2016; but see McCann, 1997). The forests that remain are predominantly montane forests which are part of the Eastern Afromontane Biodiversity Hotspot, indicating their importance in terms of biodiversity and ecosystem services (Mittermeier et al., 2011). One globally important ecosystem service, provided by intact Ethiopian montane forests, is the supply of genetic resources of wild *Coffea arabica* (Anthony et al., 2002). Whereas various drivers, including agricultural expansion and logging for construction and fuel wood have been linked to deforestation in Ethiopia (Assefa and Bork, 2014; Dessie and Kleman, 2007), the occurrence of wild *C. arabica* has played a significant role in mitigating deforestation rates of Ethiopian moist montane forests (Getahun et al., 2013; Hylander et al., 2013; Tadesse et al., 2014a). The high economic value of Arabica coffee at the world market (ICO, 2018; IMF, 2018) stimulated farmers to conserve parts of these forests for coffee production. As a forest shrub, growing naturally under a dense canopy layer, *C. arabica* depends on shade for optimal growing conditions, hence it has been traditionally cultivated under a relatively dense and species rich canopy cover (Schmitt et al., 2010).

In response to the increasing global coffee demand and human population growth, farmers aim to continuously increase coffee production, at the expense of forest integrity (Decuyper et al., 2018). To boost productivity, farmers increase space and light conditions for the cultivated coffee shrubs. Competing understorey vegetation is removed and trees are selectively cut, systematically taking out the tallest individuals or unwanted species and selecting for preferred shade providing species (Aerts et al., 2011; Schmitt et al., 2010). Reduced shade levels dramatically increase short-term coffee yields, from a mere 15 kg ha⁻¹ in natural forests annually (Schmitt et al., 2010) to 1.7–2.6 metric tonnes ha⁻¹ year⁻¹ in intensively managed systems (Aerts et al., 2011). Preferred shade

providing trees within Ethiopian *C. arabica* production systems are, for example, *Albizia gummifera* and *Albizia schimperiana* which are leguminous trees with a slim trunk and an open, wide-spreading crown, covering an as wide as possible area per trunk (Aerts et al., 2011).

There is increasing evidence of the negative impact of coffee production intensification on the diversity and abundance of forest (specialist) species and on forest structure. Previous studies in Ethiopia have reported a reduced tree and shrub species richness and abundance (Aerts et al., 2011, 2013b; Schmitt et al., 2010; Senbeta and Denich, 2006; Tadesse et al., 2014a), a degraded forest structure (Decuyper et al., 2018), a reduced carbon sequestration capacity (De Beenhouwer et al., 2016), a reduced genetic variation and altered population genetic structure in *C. arabica* (Aerts et al., 2013a; Berecha et al., 2014), and a reduced species richness of epiphytic orchids (De Beenhouwer et al., 2015a; Hundera et al., 2013), specialist forest birds (Gove et al., 2008), insects (Berecha et al., 2015; Geeraert et al., 2018; Jha and Vandermeer, 2010; Samnegård et al., 2014), and mycorrhizal fungi (De Beenhouwer et al., 2015b).

All the above mentioned evidence of negative effects of forest degradation through coffee cultivation is based on chronosequences and associated space-for-time substitution, comparing forests with different management regimes in terms of intensity of coffee cultivation. Even though chronosequences can offer invaluable insights in the ongoing processes (Pickett, 1989; Walker et al., 2010), this indirect approach for measuring temporal dynamics does not provide any information regarding the rate of degradation. In addition, results from space for time substitutions may also partly be caused by differences in local environmental conditions and initial site heterogeneity (Johnson and Miyanishi, 2008; Walker et al., 2010).

Therefore, we compiled a unique dataset of 32 plots (20m × 20m) located in Ethiopian moist Afromontane forest remnants that were surveyed in 2009 and resurveyed in 2017, using standardized methods. This approach allows an accurate quantification of the forest degradation rate caused by forest management for coffee production. We evaluated changes over time in terms of (1) species richness and diversity of woody vegetation and (2) forest structure, as quantified by woody vegetation density, basal area, and overall and dominant tree height.

2. Materials and methods

2.1. Study area

We conducted our research in the highlands of southwestern Ethiopia, in the Mana district (administrative center: Yebu, 7°45'08" N, 36°45'51" E) within the Jimma zone, Oromia region (Fig. 1). The Jimma zone is one of the major Arabica coffee growing zones in Ethiopia. The study landscape was composed of a mosaic of managed coffee forests, annual-crop agricultural land, wood lots for timber production (*Eucalyptus* and *Cupressus*), grazing lands, riverine wetland, and small human settlements. Crops cultivated in the landscape matrix include maize, teff (*Eragrostis tef*), khat (*Catha edulis*), and enset (*Ensete ventricosum*). Ethiopia has a complex forest history (Ameha et al., 2014; McCann, 1997), and due to the lack of historical information it is difficult to know the exact forest cover dynamics within our particular study area. Therefore, it might be possible that at some point in history the original forest cover in our study area already has been subjected to, and recovered from, severe human disturbances. In 2009, local elders stated that the forest was relatively intact ca. 70 years ago, with few coffee shrubs and only sparse human settlement. During both survey years, we noticed remnant canopy trees that are characteristic of natural moist Afromontane forests (e.g., *Pouteria adolfi-friedericii*, *Prunus africanus*, *Schefflera abyssinica*), within and in between the forest fragments of the study area, indicating the former presence of a larger and less disturbed moist Afromontane forest (Aerts et al., 2011). After the recognition of coffee's economic importance and its role in sustaining local livelihood, ca. 70 years ago, farmers started to manage the forest to improve coffee productivity (G. Berecha, 2017, personal observation). The soils are Nitisols. Average annual temperatures are 26 °C during daytime and 13 °C at night. Average annual rainfall is 2008 mm.

The studied forest fragments were all managed by local small-holder farmers for coffee production, and were already in the process of degradation in terms of species composition and forest structure during the first survey in 2009 (Aerts et al., 2011). Management included pruning and stumping of the coffee shrubs, removal of epiphytes that grow on the stem and branches, replacing old

or dead shrubs by locally cultivated coffee seedlings, and slashing the understorey seedlings and weeds once or twice per year. A slight variation in intensity of pruning the coffee shrubs and clearing the understorey was visible, across forests, depending on availability of labor and on experience and knowledge of the farmers about enhancing coffee productivity.

2.2. Study design

A total of 32 forest inventory plots (20×20 m) were surveyed within 24 Afromontane forest fragments that were managed for coffee production (Fig. 1). Forest fragment shapes were digitized and surface areas were calculated in QGIS (QGIS Development Team, 2015). The fragments' surface areas ranged from 0.2 to 93.0 ha (median: 2.1 ha, IQR: 6.8 ha). The plots were established and surveyed for a first time in August 2009 for a study that compared differences in woody species composition, forest structure, and regeneration potential among forests with different management regimes in terms of coffee cultivation intensity (Aerts et al., 2013b). In August 2017, we resurveyed the plots using standardized methods. The original plots were aligned on the Ethiopian national grid (UTM 37N on Adindan datum) with plot boundaries following north-south and east-west orientations. The plots were relocated by use of GPS coordinates (Oregon 700 Garmin) of the southwestern corner of each plot. From this point, we reconstructed the plot toward the north and east by use of compass and measuring tape. Within each plot, abundance and height of all tree and shrub species with a diameter at breast height (DBH) ≥ 5 cm were measured, *C. arabica* shrubs not included. Tree and shrub heights were measured according to the 'angle-measure method' (also called the 'tangent method') (Korning and Thomsen, 1994) with a mechanical clinometer to measure the angles, and a measuring tape to measure the horizontal distance between the observer and the base of the tree. The observer was careful to make a good estimation of the tree top, by standing at a distance as far as possible from the tree. For flat topped trees, the clinometer was aimed at the central point of the upper canopy and not at the edge to avoid overestimation of tree height. Species were identified by local specialists and with the help of literature by Dharani (2002) and Fichtl and Admasu (1994). *Acacia* (*Vachellia/Senegalial*¹) and *Albizia* species were identified up to genus level, all other species were identified to species level.

2.3. Data analysis

Woody vegetation diversity and forest structure were assessed in 32 plots in 2009 and 2017. We evaluated differences between both years, based on following response variables: Hill's N_0 (i.e., species richness), Hill's N_1 (i.e., exponential of Shannon entropy), Hill's N_2 (i.e., inverse Simpson concentration), woody vegetation density, basal area, and overall and dominant tree height. Hill's N_0 and tree height were directly measured in the field. Hill's N_1 and Hill's N_2 were calculated based on the species abundance data (Chao et al., 2014), using the '*ChaoShannon*' and '*Chaosimpson*' functions, respectively, of the iNEXT package (Hsieh et al., 2016) in R (R Core Team, 2018). Tree and shrub density per hectare was calculated based on the measured abundance on plot level (400 m²). Basal area (m²/ha) was calculated based on the DBH of the measured trees and shrubs per plot. Dominant tree height is defined as the average height of the five tallest trees in the plot.

To evaluate differences in woody vegetation and forest structure between both survey years, we applied generalized linear mixed models. We included 'year' (i.e., 2009 or 2017) as a fixed factor, and 'fragment size' (i.e., surface area in ha, continuous variable) as a covariate in the models. We also included the 'year $\times$ fragment size' interaction to evaluate potential differential time effects for fragments of different surface areas. As plots were clustered in 24 forest fragments, we included fragment identity as a random factor in the models to account for pseudo-replication in statistical analyses. Furthermore, we also included plot ID as a random intercept to take into account the repeated measures design (paired data). The models took following form:

response variable $\sim$ *year* + *fragment size* + *year* $\times$ *fragment size* + (1 | *fragment*) + (1 | *plot*).

The response variables Hill's N_0 and tree density comprised discrete, positive, right skewed data. Consequently, we modelled Hill's N_0 using the Poisson probability distribution and a log link function, which is considered the most appropriate distribution for this type of data in the absence of

¹ African *Acacia* species with spinescent stipules (thorns) have been regrouped in the new genus *Vachellia* and those without thorns in *Senegalial* as the genus name *Acacia* is now reserved for species indigenous to Australia (Dyer, 2014). For the sake of clarity we have maintained the former genus name *Acacia*.

overdispersion (overdispersion: $\chi^2 = 28.88$, $p = 0.999$). Tree density, on the other hand, was modelled using a negative binomial probability distribution with log link function, due to significant overdispersion ($\chi^2 = 332.76$, $p < 0.001$). The other response variables (i.e., Hill's N_1 , Hill's N_2 , basal area, and overall and dominant tree height) comprised positive, continuous, right skewed data. Therefore, these variables were modelled using the Gamma probability distribution with inverse link function. We reduced each full model through backward stepwise model selection based on ΔAIC , and calculated estimated marginal means (EMMs) for each response variable, for each survey year.

We tested for differences in community composition between the two survey years by performing canonical redundancy analysis (RDA). First, we removed the variation attributed to the specific plot using the 'Condition' statement in the RDA model, and then we explicitly tested for the variable 'year' (i.e., 2009 or 2017). We tested for significance based on 1000 permutations. As 2009 and 2017 survey years were paired within each survey plot, we restricted permutations of samples within plots. We, furthermore, visualized potential vegetation changes of the tree and shrub community composition in both time points and across all plots, using a non-metric multidimensional scaling (NMDS) ordination with Bray-Curtis distances on the tree and shrub community composition (*plot* $\times$ *species abundance* matrix). A three-axis solution provided a stress level (0.13) below the threshold (0.20).

We performed all analyses in R, version 3.5.1 (R Core Team, 2018). Poisson and Gamma-distributed models were performed using the 'glmer' function in the lme4 package (Bates et al., 2015). To model the negative binomial probability distribution, we used 'glmmTMB', glmmTMB package (Brooks et al., 2017). Estimated marginal means were calculated using 'emmeans', emmeans package (Lenth, 2018). We used the vegan package (Oksanen et al., 2018) to perform the RDA ('rda'), permutation test ('anova.cca'), and NMDS ordination ('metaMDS'). The 'how' function, vegan package, was used to restrict permutations of samples only within plots ('blocks' = plot). Figures were made using the ggplot2 package (Wickham, 2016).

3. Results

3.1. Woody vegetation diversity and forest structure

A total of 263 trees and shrubs (DBH ≥ 5 cm) and 29 different species, was recorded in 2009, and a total of 181 trees and shrubs belonging to 20 species was recorded in 2017 (Fig. S1, Table S1). For both stem number and number of species, this is equivalent to a reduction of 31% over eight years. Hill's N_0 was reduced by 23% ($\chi^2 = 3.47$, $p = 0.063$), and both Hill's N_1 and Hill's N_2 were reduced by 14% ($\chi^2 = 13.22$, $p < 0.001$; $\chi^2 = 16.04$, $p < 0.001$, respectively; Fig. 2A, Table 1). The forest structure differed between 2009 and 2017 with respect to woody vegetation density, and overall tree and shrub height (Fig. 2B,D; Table 1). Density reduced over time by 31% ($z = -3.39$, $p < 0.001$). Overall tree and shrub height increased over time with 11% ($\chi^2 = 6.79$, $p = 0.009$). No significant changes were found for basal area ($\chi^2 = 0.03$, $p = 0.866$) and dominant tree height ($\chi^2 = 0.93$, $p = 0.761$; Fig. 2C,D; Table 1). Full and reduced models are reported in Tables S4 and S5, respectively.

3.2. Community composition

The dominant woody species in both survey years were *Albizia* spp. (34% and 40% of the total observed abundance in 2009 and 2017, respectively), *Croton macrostachyus* (16% in 2009; 23% in 2017) and *Millettia ferruginea* (10% in 2009; 7% in 2017; Table S1). Group separation based on survey year was not significant following the RDA analysis ($F_{1,31} = 0.96$, $p = 0.410$). NMDS ordination of the 2009 and 2017 woody community compositions showed a large overlap rather than two distinct clusters (Fig. 3A, Fig. S3). A small shift of the confidence ellipses for both years is visible towards the upper right corner of the ordination plot. This shift corresponds with an increased dominance of *Albizia* species over time (Fig. 3B; Fig. S2B; Table S2,S3).

4. Discussion

4.1. Rapid progress of Afromontane forest degradation

Although the studied Afromontane forest remnants appeared as unchanged between 2009 and 2017 in terms of shape, surface area, or degree of isolation as seen on satellite images (e.g., Google Earth, Fig. S4), our results showed a further degradation of forest structure over an eight-year period. We found a reduction in woody vegetation density, species richness, and diversity, while the overall tree height increased, and the basal area and dominant tree height remained unchanged. These findings seem consistent with a low thinning regime where farmers remove predominantly intermediate and suppressed trees from the understorey (Kraft crown classes 4-5), which would otherwise provide unwanted, additional shading of coffee shrubs.

Similar magnitudes of reductions in woody vegetation density, species richness and diversity have also been reported by studies comparing coffee forests with different management intensities in SW Ethiopia (Aerts et al., 2011, 2013b; De Beenhouwer et al., 2016; Schmitt et al., 2010; Senbeta and Denich, 2006). Yet, to the best of our knowledge, our study is the first to elucidate the degradation rate of moist Afromontane forests that are managed for coffee production, over an eight-year period. Furthermore, in contrast to space-for-time substitutions, our analysis at two time points allows for an accurate assessment of changes in woody vegetation diversity and forest structure due to coffee cultivation, without potential confounding effects of different local environmental conditions such as altitude and rainfall which often co-vary with the geographical location of coffee forests of different management intensity in our study region (De Beenhouwer et al., 2016; Walker et al., 2010).

4.2. Ecosystem effects

Thinning improves light conditions in the understorey, not only for coffee and early-successional tree species but also for annual weeds such as *Bidens* sp. which further entices farmers to slash the understorey on a regular basis. Thinning generally reduces the conditions for the succession of shade-tolerant, late successional species of the moist Afromontane forest. Seedling and sapling density of early-successional tree species such as *Albizia* spp. and *M. ferruginea* usually rapidly increase after thinning, but as these are removed by regular slashing, long term crown cover cannot be guaranteed in these forest fragments (Hundera et al., 2015). Previously, farmers already selected the desired amounts of shade, by managing the original Afromontane forest canopy according to a high thinning regime, where trees from the dominant and codominant height classes (Kraft crown classes 1-2) were removed systematically to favor the preferred shade providing tree species such as *Albizia* spp., *C. macrostachyus*, and *M. ferruginea* (Aerts et al., 2011; Belay et al., 2018; Schmitt et al., 2010). Along with a decreasing tree and shrub density and diversity over time, we also observed a further increase in dominance of *Albizia* spp. and *C. macrostachyus*. This indicates that farmers continued to select for a minimum of shade providing species, with the aim to further increase coffee yield.

As forest degradation is positively related to reduced habitat size and increased edge effects (Ewers and Didham, 2005; Ferraz et al., 2007; Haddad et al., 2015), we expected that temporal changes in woody vegetation diversity and forest structure may be less pronounced within the larger fragments in our study area as compared to the smaller fragments. However, in our study we did not find an effect of the different forest fragment sizes in which the survey plots were located. This indicates that the farmers applied a low thinning in an equal magnitude over the whole landscape. As the remaining tree and shrub species have grown over time, the appearance of new tree or shrub individuals in the 2017 survey can be explained by the fact that these individuals were too small (DBH < 5 cm) to be included in the 2009 survey. However, some of these new occurrences could be an effect of potential relocation errors as relocation of the plots was based on GPS coordinates.

With continued management for coffee production, forest degradation continues and unavoidably affects ecosystem functioning and related services (Edwards, 2016). Earlier studies found significant losses of aboveground C-stocks when comparing intact Ethiopian moist Afromontane forests with managed coffee forests through space-for-time substitutions (De Beenhouwer et al., 2016; Vanderhaegen et al., 2015). It is known that massive losses of carbon occur with the removal of large, old trees (Keith et al., 2009; Sist et al., 2014; Stephenson et al., 2014), which are also known to provide several other important ecosystem services, e.g., maintaining microclimatic conditions, nutrient and water cycling, and biodiversity conservation (Lindenmayer et al., 2014; Lindenmayer and Laurance, 2017). The results of our study suggest a continuation in the Ethiopian moist Afromontane forests' loss of C-storage capacity and woody vegetation diversity under a low thinning regime for coffee cultivation.

4.3. Indirect effects on coffee production

Degraded moist Afromontane coffee forests still maintain a higher vegetation diversity compared to other perennial crop systems (e.g., Khat (*Catha edulis*), Eucalyptus trees) or annual-crop systems (Hylander and Nemomissa, 2008; Jara et al., 2017). By providing islands of tree cover in an otherwise open agricultural landscape, it has been acknowledged that even degraded forest fragments make a valuable contribution to the landscape's biodiversity (Bhagwat et al., 2008; Muñoz et al., 2013). However, at the forest level, the reduced complexity in forest structure and a reduced woody vegetation diversity are expected to have a negative impact on the fragment's overall biodiversity, including the coffee pollinator community (Berecha et al., 2015; Geeraert et al., 2018; Klein et al., 2002; Samnegård et al., 2014). The negative effects of reduced pollinator diversity on coffee yield have been discussed before, for example, in the context of coffee production systems in Indonesia (Klein et al., 2003) and Central America (Ricketts et al., 2004; Roubik, 2002; Vergara and Badano, 2009).

Even though short-term higher coffee yields may be obtained when shade is reduced, shade has beneficial effects on coffee quality through reduced light conditions (Geromel et al., 2008), reduced mean air temperatures (Bertrand et al., 2012; Joët et al., 2010), increased relative soil humidity (De Beenhouwer et al., 2015b), and a lower degree of soil erosion and nutrient leaching (Babbar and Zak, 1994). Previous research in SW Ethiopia showed an impoverishment of organoleptic quality of *C. arabica* beans with increasing forest management intensity (Geeraert et al., 2019). Also long-term yield stability benefits from shade through the reduction of alternate bearing and risk of over-bearing (Vaast et al., 2006).

4.4. Implications for conservation

The rapid forest degradation progress found in our study, in already strongly managed forest remnants, suggests that Afromontane forest remnants with less intensified management may suffer from even higher degradation rates since their coffee yield could be increased more easily through reduction of shade levels. Therefore, our study emphasizes the need for conservation of the remaining moist Afromontane forests and their valuable biodiversity and ecosystem services, such as the provisioning of Arabica coffee's genetic resources.

To halt further forest degradation through coffee cultivation, implementation of REDD+ (Reducing Emissions from Deforestation and Forest Degradation, plus the conservation, sustainable management and enhancement of forest carbon stocks) and related policy frameworks could be an option. These frameworks are designed to reduce atmospheric CO₂ emissions from deforestation and forest degradation, and may also result in co-benefits for biodiversity and other ecosystem services (Imai et al., 2014; Sullivan et al., 2017; Venter, 2014). Furthermore, several coffee certification programs aim to compensate farmers for loss of income when forest management is reduced in favor of the local biodiversity (Mitiku et al., 2018). However, premium coffee prices do often not sufficiently compensate for the related yield losses (Mitiku et al., 2017; Perfecto et al., 2005; Vanderhaegen et al., 2018), and in the unique case of Ethiopia, where coffee is a natural understorey species, coffee certification programs may actually be an incentive to convert natural forests into strongly managed yet certified coffee forests (Gove et al., 2008; Hylander et al., 2013).

Under a continued low thinning regime of the studied remnant moist Afromontane forest fragments, the species poor canopy is expected to be conserved, while smaller trees in the understorey will continue to be removed, resulting in additional diversity losses. Conversion of existing degraded forest remnants to more natural Afromontane forest could be achieved through high thinning (e.g., removing some *Albizia* trees from the upper canopy), which would allow other light-demanding species to reach the upper canopy. Reduced slashing, would be another option, allowing shade-demanding species to recruit into the upper canopy, if mature mother trees of such species are still present in, or near, the degraded forest fragments. A number of indigenous tree species (e.g., *Allophylus abyssinicus*, *Ekebergia capensis*, *Prunus africana* and *Syzygium guineense*) provides important ecosystem services such as food, medicine and bee forage in addition to shade for coffee (Teketay et al., 2010). Assisting regeneration of such multipurpose tree species through fencing, seeding or planting of seedlings is also a viable option to restore moist Afromontane forest (Hundera

et al., 2015). Nevertheless, the willingness of farmers to adopt such forest management practices remains to be evaluated in the field.

5. Reference list

- Aerts, R., Berecha, G., Gijbels, P., Hundera, K., Van Glabeke, S., Vandepitte, K., Muys, B., Roldán-Ruiz, I., Honnay, O., 2013a. Genetic variation and risks of introgression in the wild *Coffea arabica* gene pool in south-western Ethiopian montane rainforests. *Evol. Appl.* 6, 243–252. <https://doi.org/10.1111/j.1752-4571.2012.00285.x>
- Aerts, R., Hundera, K., Berecha, G., Gijbels, P., Baeten, M., Van Mechelen, M., Hermy, M., Muys, B., Honnay, O., 2011. Semi-forest coffee cultivation and the conservation of Ethiopian Afromontane rainforest fragments. *For. Ecol. Manage.* 261, 1034–1041. <https://doi.org/10.1016/j.foreco.2010.12.025>
- Aerts, R., Hundera, K., Fontaine, A., Van Mechelen, M., Gijbels, P., Honnay, O., Muys, B., 2013b. Effects of coffee management intensity on composition, structure, and regeneration status of Ethiopian moist evergreen afromontane forests. *Environ. Manage.* 51, 801–809. <https://doi.org/10.1007/s00267-012-9976-5>
- Aleman, J.C., Jarzyna, M.A., Staver, A.C., 2018. Forest extent and deforestation in tropical Africa since 1900. *Nat. Ecol. Evol.* 2, 26–33. <https://doi.org/10.1038/s41559-017-0406-1>
- Ameha, A., Larsen, H.O., Lemenih, M., 2014. Participatory forest management in Ethiopia: Learning from pilot projects. *Environ. Manage.* 53, 838–854. <https://doi.org/10.1007/s00267-014-0243-9>
- Anthony, F., Combes, M.C., Astorga, C., Bertrand, B., Graziosi, G., Lashermes, P., 2002. The origin of cultivated *Coffea arabica* L. varieties revealed by AFLP and SSR markers. *Theor. Appl. Genet.* 104, 894–900. <https://doi.org/10.1007/s00122-001-0798-8>
- Assefa, E., Bork, H.-R., 2014. Deforestation and forest management in southern Ethiopia: Investigations in the Chenchu and Arbaminch areas. *Environ. Manage.* 53, 284–299. <https://doi.org/10.1007/s00267-013-0182-x>
- Babbar, L.I., Zak, D.R., 1994. Nitrogen cycling in coffee agroecosystems: Net N mineralization and nitrification in the presence and absence of shade trees. *Agric. Ecosyst. Environ.* 48, 107–113. [https://doi.org/10.1016/0167-8809\(94\)90081-7](https://doi.org/10.1016/0167-8809(94)90081-7)
- Baccini, A., Walker, W., Carvalho, L., Farina, M., Sulla-Menashe, D., Houghton, R.A., 2017. Tropical forests are a net carbon source based on aboveground measurements of gain and loss. *Science* (80-.). 358, 230–234. <https://doi.org/10.1126/science.aam5962>
- Barlow, J., Lennox, G.D., Ferreira, J., Berenguer, E., Lees, A.C., Nally, R. Mac, Thomson, J.R., Ferraz, S.F. de B., Louzada, J., Oliveira, V.H.F., Parry, L., Ribeiro de Castro Solar, R., Vieira, I.C.G., Aragão, L.E.O.C., Begotti, R.A., Braga, R.F., Cardoso, T.M., Jr, R.C. de O., Souza Jr, C.M., Moura, N.G., Nunes, S.S., Siqueira, J.V., Pardini, R., Silveira, J.M., Vaz-de-Mello, F.Z., Veiga, R.C.S., Venturieri, A., Gardner, T.A., 2016. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature* 535, 144–147. <https://doi.org/10.1038/nature18326>
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.* 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Belay, B., Zewdie, S., Mekuria, W., Abiyu, A., Amare, D., Woldemariam, T., 2018. Woody species diversity and coffee production in remnant semi-natural dry Afromontane Forest in Zegie Peninsula, Ethiopia. *Agrofor. Syst.* <https://doi.org/10.1007/s10457-018-0285-8>
- Berecha, G., Aerts, R., Muys, B., Honnay, O., 2015. Fragmentation and management of Ethiopian moist evergreen forest drive compositional shifts of insect communities visiting wild Arabica coffee flowers. *Environ. Manage.* 55, 373–382. <https://doi.org/10.1007/s00267-014-0393-9>
- Berecha, G., Aerts, R., Vandepitte, K., Van Glabeke, S., Muys, B., Roldán-Ruiz, I., Honnay, O., 2014. Effects of forest management on mating patterns, pollen flow and intergenerational transfer of genetic diversity in wild Arabica coffee (*Coffea arabica* L.) from Afromontane rainforests. *Biol. J. Linn. Soc.* 112, 76–88. <https://doi.org/10.1111/bij.12274>
- Bertrand, B., Boulanger, R., Dussert, S., Ribeyre, F., Berthiot, L., Descroix, F., Joët, T., 2012.

- Climatic factors directly impact the volatile organic compound fingerprint in green Arabica coffee bean as well as coffee beverage quality. *Food Chem.* 135, 2575–2583. <https://doi.org/10.1016/j.foodchem.2012.06.060>
- Bhagwat, S.A., Willis, K.J., Birks, H.J.B., Whittaker, R.J., 2008. Agroforestry: a refuge for tropical biodiversity? *Trends Ecol. Evol.* 23, 261–267. <https://doi.org/10.1016/j.tree.2008.01.005>
- Bishaw, B., 2001. Deforestation and land degradation in the Ethiopian highlands: A strategy for physical recovery. *Northeast Afr. Stud.* 8, 7–25. <https://doi.org/10.1353/nas.2005.0014>
- Brooks, M.E., Kristensen, K., Koen J. van Benthem, A.M., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* 9, 378–400.
- Burivalova, Z., Şekercioğlu, Ç.H., Koh, L.P., 2014. Thresholds of logging intensity to maintain tropical forest biodiversity. *Curr. Biol.* 24, 1893–1898. <https://doi.org/10.1016/j.cub.2014.06.065>
- Cardinale, B.J., Gonzalez, A., Allington, G.R.H., Loreau, M., 2018. Is local biodiversity declining or not? A summary of the debate over analysis of species richness time trends. *Biol. Conserv.* 219, 175–183. <https://doi.org/10.1016/j.biocon.2017.12.021>
- Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., Ellison, A.M., 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecol. Monogr.* 84, 45–67. <https://doi.org/10.1890/13-0133.1>
- Cochrane, M.A., 2003. Fire science for rainforests. *Nature* 421, 913–919. <https://doi.org/10.1038/nature01437>
- Curtis, P.G., Slay, C.M., Harris, N.L., Tyukavina, A., Hansen, M.C., 2018. Classifying drivers of global forest loss. *Science (80-.)*. 361, 1108–1111. <https://doi.org/10.1126/science.aau3445>
- Daily, G.C., 1997. *Nature's services: Societal dependence on natural ecosystems*. Cambridge University Press, Washington, DC.
- De Beenhouwer, M., Aerts, R., Hundera, K., Van Overtveld, K., Honnay, O., 2015a. Management intensification in Ethiopian coffee forests is associated with crown habitat contraction and loss of specialized epiphytic orchid species. *Basic Appl. Ecol.* 16, 592–600. <https://doi.org/10.1016/j.baae.2015.06.006>
- De Beenhouwer, M., Geeraert, L., Mertens, J.E.J., Van Geel, M., Aerts, R., Vanderhaegen, K., Honnay, O., 2016. Biodiversity and carbon storage co-benefits of coffee agroforestry across a gradient of increasing management intensity in the SW Ethiopian highlands. *Agric. Ecosyst. Environ.* 222, 193–199. <https://doi.org/10.1016/j.agee.2016.02.017>
- De Beenhouwer, M., Muleta, D., Peeters, B., Van Geel, M., Lievens, B., Honnay, O., 2015b. DNA pyrosequencing evidence for large diversity differences between natural and managed coffee mycorrhizal fungal communities. *Agron. Sustain. Dev.* 35, 241–249. <https://doi.org/10.1007/s13593-014-0231-8>
- Decuyper, M., Mulatu, K.A., Brede, B., Calders, K., Armston, J., Rozendaal, D.M.A., Mora, B., Clevers, J.G.P.W., Kooistra, L., Herold, M., Bongers, F., 2018. Assessing the structural differences between tropical forest types using Terrestrial Laser Scanning. *For. Ecol. Manage.* 429, 327–335. <https://doi.org/10.1016/j.foreco.2018.07.032>
- Dessie, G., Kleman, J., 2007. Pattern and magnitude of deforestation in the South Central Rift Valley region of Ethiopia. *Mt. Res. Dev.* 27, 162–168. <https://doi.org/10.1659/mrd.0730>
- DeVries, B., Verbesselt, J., Kooistra, L., Herold, M., 2015. Robust monitoring of small-scale forest disturbances in a tropical montane forest using Landsat time series. *Remote Sens. Environ.* 161, 107–121. <https://doi.org/10.1016/j.rse.2015.02.012>
- Dharani, N., 2002. *Guide to common trees and shrubs of East Africa*, 1st ed. Struik Publishers, Cape Town (South Africa).
- Dyer, C., 2014. New names for the African *Acacia* species in *Vachellia* and *Senegalia*. *South. For. a J. For. Sci.* 76, iii–iii. <https://doi.org/10.2989/20702620.2014.980090>
- Edwards, D.P., 2016. The rainforest's “do not disturb” signs. *Nature* 535, 44–45. <https://doi.org/10.1038/nature18901>
- Ewers, R.M., Didham, R.K., 2005. Confounding factors in the detection of species responses to habitat fragmentation. *Biol. Rev.* 81, 117. <https://doi.org/10.1017/S1464793105006949>
- Fahrig, L., Arroyo-Rodríguez, V., Bennett, J.R., Boucher-Lalonde, V., Cazetta, E., Currie, D.J., Eigenbrod, F., Ford, A.T., Harrison, S.P., Jaeger, J.A.G., Koper, N., Martin, A.E., Martin, J.-L.,

- Metzger, J.P., Morrison, P., Rhodes, J.R., Saunders, D.A., Simberloff, D., Smith, A.C., Tischendorf, L., Vellend, M., Watling, J.I., 2019. Is habitat fragmentation bad for biodiversity? *Biol. Conserv.* 230, 179–186. <https://doi.org/10.1016/j.biocon.2018.12.026>
- Ferraz, G., Nichols, J.D., Hines, J.E., Stouffer, P.C., Bierregaard, R.O., Lovejoy, T.E., 2007. A large-scale deforestation experiment: Effects of patch area and isolation on Amazon birds. *Science* (80-.). 315, 238–241. <https://doi.org/10.1126/science.1133097>
- Fichtl, R., Admasu, A., 1994. Honeybee flora of Ethiopia, 1st ed. Margraf Verlag, Weikersheim (Germany).
- Fletcher, R.J., Didham, R.K., Banks-Leite, C., Barlow, J., Ewers, R.M., Rosindell, J., Holt, R.D., Gonzalez, A., Pardini, R., Damschen, E.I., Melo, F.P.L., Ries, L., Prevedello, J.A., Tscharntke, T., Laurance, W.F., Lovejoy, T., Haddad, N.M., 2018. Is habitat fragmentation good for biodiversity? *Biol. Conserv.* 226, 9–15. <https://doi.org/10.1016/j.biocon.2018.07.022>
- Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global consequences of land use. *Science* (80-.). 309, 570–574. <https://doi.org/10.1126/science.1111772>
- Geeraert, L., Aerts, R., Jordaens, K., Dox, I., Wellens, S., Couri, M., Berecha, G., Honnay, O., 2018. Intensification of Ethiopian coffee agroforestry drives impoverishment of the Arabica coffee flower visiting bee and fly communities. *Agrofor. Syst.* <https://doi.org/10.1007/s10457-018-0280-0>
- Geeraert, L., Berecha, G., Honnay, O., Aerts, R., 2019. Organoleptic quality of Ethiopian Arabica coffee deteriorates with increasing intensity of coffee forest management. *J. Environ. Manage.* 231, 282–288. <https://doi.org/10.1016/j.jenvman.2018.10.037>
- Geromel, C., Ferreira, L.P., Davrieux, F., Guyot, B., Ribeyre, F., dos Santos Scholz, M.B., Pereira, L.F.P., Vaast, P., Pot, D., Leroy, T., Filho, A.A., Vieira, L.G.E., Mazzafera, P., Marraccini, P., 2008. Effects of shade on the development and sugar metabolism of coffee (*Coffea arabica* L.) fruits. *Plant Physiol. Biochem.* 46, 569–579. <https://doi.org/10.1016/j.plaphy.2008.02.006>
- Getahun, K., Rompaey, A. Van, Turnhout, P. Van, Poesen, J., 2013. Factors controlling patterns of deforestation in moist evergreen Afromontane forests of Southwest Ethiopia. *For. Ecol. Manage.* 304, 171–181. <https://doi.org/10.1016/j.foreco.2013.05.001>
- Gibbs, H.K., Ruesch, A.S., Achard, F., Clayton, M.K., Holmgren, P., Ramankutty, N., Foley, J.A., 2010. Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. *Proc. Natl. Acad. Sci.* 107, 16732–16737. <https://doi.org/10.1073/pnas.0910275107>
- Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E., Sodhi, N.S., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478, 378–381. <https://doi.org/10.1038/nature10425>
- Gove, A.D., Hylander, K., Nemomisa, S., Shimelis, A., 2008. Ethiopian coffee cultivation - Implications for bird conservation and environmental certification. *Conserv. Lett.* 1, 208–216. <https://doi.org/10.1111/j.1755-263X.2008.00033.x>
- Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.-X., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* 1, 1–9. <https://doi.org/10.1126/sciadv.1500052>
- Hansen, M.C., Potapov, P. V, Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S. V, Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., Townshend, J.R.G., 2013. High-resolution global maps of 21st-century forest cover change. *Science* (80-.). 342, 850–853. <https://doi.org/10.1126/science.1244693>
- Hosonuma, N., Herold, M., De Sy, V., De Fries, R.S., Brockhaus, M., Verchot, L., Angelsen, A., Romijn, E., 2012. An assessment of deforestation and forest degradation drivers in developing countries. *Environ. Res. Lett.* 7, 044009. <https://doi.org/10.1088/1748-9326/7/4/044009>
- Hsieh, T.C., Ma, K.H., Chao, A., 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods Ecol. Evol.* 7, 1451–1456. <https://doi.org/10.1111/2041-210X.12613>

- Hundera, K., Aerts, R., De Beenhouwer, M., Van Overtveld, K., Helsen, K., Muys, B., Honnay, O., 2013. Both forest fragmentation and coffee cultivation negatively affect epiphytic orchid diversity in Ethiopian moist evergreen Afromontane forests. *Biol. Conserv.* 159, 285–291. <https://doi.org/10.1016/j.biocon.2012.10.029>
- Hundera, K., Honnay, O., Aerts, R., Muys, B., 2015. The potential of small exclosures in assisting regeneration of coffee shade trees in South-Western Ethiopian coffee forests. *Afr. J. Ecol.* 53, 389–397. <https://doi.org/10.1111/aje.12203>
- Hylander, K., Nemomissa, S., 2008. Home garden coffee as a repository of epiphyte biodiversity in Ethiopia. *Front. Ecol. Environ.* 6, 524–528. <https://doi.org/10.1890/080001>
- Hylander, K., Nemomissa, S., Delrue, J., Enkosa, W., 2013. Effects of coffee management on deforestation rates and forest integrity. *Conserv. Biol.* 27, 1031–1040. <https://doi.org/10.1111/cobi.12079>
- ICO, 2018. Coffee Market Report: December 2018. International Coffee Organization (Downloaded from <http://www.ico.org/Market-Report-18-19-e.asp>).
- Imai, N., Tanaka, A., Samejima, H., Sugau, J.B., Pereira, J.T., Titin, J., Kurniawan, Y., Kitayama, K., 2014. Tree community composition as an indicator in biodiversity monitoring of REDD+. *For. Ecol. Manage.* 313, 169–179. <https://doi.org/10.1016/j.foreco.2013.10.041>
- IMF, 2018. The Federal Democratic Republic of Ethiopia: IMF country report December 2018. International Monetary Fund country report No. 18/354 (Downloaded from <https://www.imf.org/en/Publications/Search?series=IMF+Staff+Country+Reports&when=During&year=2018&title=E>).
- Jara, T., Hylander, K., Nemomissa, S., 2017. Tree diversity across different tropical agricultural land use types. *Agric. Ecosyst. Environ.* 240, 92–100. <https://doi.org/10.1016/j.agee.2017.01.042>
- Jha, S., Vandermeer, J.H., 2010. Impacts of coffee agroforestry management on tropical bee communities. *Biol. Conserv.* 143, 1423–1431. <https://doi.org/10.1016/j.biocon.2010.03.017>
- Joët, T., Laffargue, A., Descroix, F., Doubeau, S., Bertrand, B., Kochko, A. de, Dussert, S., 2010. Influence of environmental factors, wet processing and their interactions on the biochemical composition of green Arabica coffee beans. *Food Chem.* 118, 693–701. <https://doi.org/10.1016/j.foodchem.2009.05.048>
- Johnson, E.A., Miyanishi, K., 2008. Testing the assumptions of chronosequences in succession. *Ecol. Lett.* 11, 419–431. <https://doi.org/10.1111/j.1461-0248.2008.01173.x>
- Keenan, R.J., Reams, G.A., Achard, F., de Freitas, J. V., Grainger, A., Lindquist, E., 2015. Dynamics of global forest area: Results from the FAO Global Forest Resources Assessment 2015. *For. Ecol. Manage.* 352, 9–20. <https://doi.org/10.1016/j.foreco.2015.06.014>
- Keith, H., Mackey, B.G., Lindenmayer, D.B., 2009. Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. *Proc. Natl. Acad. Sci.* 106, 11635–11640. <https://doi.org/10.1073/pnas.0901970106>
- Klein, A.-M., Steffan-Dewenter, I., Buchori, D., Tscharntke, T., 2002. Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. *Conserv. Biol.* 16, 1003–1014. <https://doi.org/10.1046/j.1523-1739.2002.00499.x>
- Klein, A.-M., Steffan-Dewenter, I., Tscharntke, T., 2003. Fruit set of highland coffee increases with the diversity of pollinating bees. *Proc. Biol. Sci.* 270, 955–61. <https://doi.org/10.1098/rspb.2002.2306>
- Korning, J., Thomsen, K., 1994. A new method for measuring tree height in tropical rain forest. *J. Veg. Sci.* 5, 139–140. <https://doi.org/10.2307/3235647>
- Lenth, R., 2018. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.3.0. (<https://CRAN.R-project.org/package=emmeans>).
- Lewis, S.L., Edwards, D.P., Galbraith, D., 2015. Increasing human dominance of tropical forests. *Science* (80-.). 349, 827–832. <https://doi.org/10.1126/science.aaa9932>
- Lindenmayer, D.B., Laurance, W.F., 2017. The ecology, distribution, conservation and management of large old trees. *Biol. Rev.* 92, 1434–1458. <https://doi.org/10.1111/brev.12290>
- Lindenmayer, D.B., Laurance, W.F., Franklin, J.F., Likens, G.E., Banks, S.C., Blanchard, W., Gibbons, P., Ikin, K., Blair, D., McBurney, L., Manning, A.D., Stein, J.A.R., 2014. New policies for old trees: Averting a global crisis in a keystone ecological structure. *Conserv. Lett.* 7, 61–69. <https://doi.org/10.1111/conl.12013>

- McCann, J.C., 1997. The plow and the forest: Narratives of deforestation in Ethiopia, 1840–1992. *Environ. Hist. Durh. N. C.* 2, 138–159. <https://doi.org/10.2307/3985505>
- MEA, 2005. Ecosystems and human well-being: Synthesis. The Millennium Ecosystem Assessment series. Island Press, Washington, DC.
- Mitiku, F., Mey, Y. de, Nyssen, J., Maertens, M., 2017. Do private sustainability standards contribute to income growth and poverty alleviation? A comparison of different coffee certification schemes in Ethiopia. *Sustain.* 9. <https://doi.org/10.3390/su9020246>
- Mitiku, F., Nyssen, J., Maertens, M., 2018. Certification of semi-forest coffee as a land-sharing strategy in Ethiopia. *Ecol. Econ.* 145, 194–204. <https://doi.org/10.1016/j.ecolecon.2017.09.008>
- Mittermeier, R.A., Turner, W.R., Larsen, F.W., Larsen Wugt, F., 2011. Biodiversity Hotspots. <https://doi.org/10.1007/978-3-642-20992-5>
- Muñoz, J.C., Aerts, R., Thijs, K.W., Stevenson, P.R., Muys, B., Sekercioglu, C.H., 2013. Contribution of woody habitat islands to the conservation of birds and their potential ecosystem services in an extensive Colombian rangeland. *Agric. Ecosyst. Environ.* 173, 13–19. <https://doi.org/10.1016/j.agee.2013.04.006>
- Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhusseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L.P., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G.M., Scharlemann, J.P.W., Purvis, A., 2015. Global effects of land use on local terrestrial biodiversity. *Nature* 520, 45–50. <https://doi.org/10.1038/nature14324>
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2018. *vegan: Community Ecology Package*. R package version 2.5-3. (<https://CRAN.R-project.org/package=vegan>).
- Peres, C.A., 2000. Effects of Subsistence Hunting on Vertebrate Community Structure in Amazonian Forests. *Conserv. Biol.* 14, 240–253. <https://doi.org/10.1046/j.1523-1739.2000.98485.x>
- Peres, C.A., Barlow, J., Laurance, W.F., 2006. Detecting anthropogenic disturbance in tropical forests. *Trends Ecol. Evol.* 21, 227–229. <https://doi.org/10.1016/j.tree.2006.03.007>
- Perfecto, I., Vandermeer, J., Mas, A., Pinto, L.S., 2005. Biodiversity, yield, and shade coffee certification. *Ecol. Econ.* 54, 435–446. <https://doi.org/10.1016/j.ecolecon.2004.10.009>
- Pickett, S.T.A., 1989. Space-for-Time Substitution as an Alternative to Long-Term Studies, in: Likens, G.E. (Ed.), *Long-Term Studies in Ecology*. Springer New York, New York, NY, pp. 110–135. https://doi.org/10.1007/978-1-4615-7358-6_5
- QGIS Development Team, 2015. QGIS Geographic Information System.
- R Core Team, 2018. R: A language and environment for statistical computing.
- Reid, R.S., Kruska, R.L., Muthui, N., Taye, A., Wotton, S., Wilson, C.J., Mulatu, W., 2000. Land-use and land-cover dynamics in response to changes in climatic, biological and socio-political forces: The case of southwestern Ethiopia. *Landsc. Ecol.* 15, 339–355. <https://doi.org/10.1023/A:1008177712995>
- Ricketts, T.H., Daily, G.C., Ehrlich, P.R., Michener, C.D., 2004. Economic value of tropical forest to coffee production. *Proc. Natl. Acad. Sci.* 101, 12579–12582.
- Roubik, D.W., 2002. The value of bees to the coffee harvest. *Nature* 417, 708. [https://doi.org/10.1002/\(SICI\)1097-0177\(199909\)216:1<1::AID-DVDY1>3.0.CO;2-T](https://doi.org/10.1002/(SICI)1097-0177(199909)216:1<1::AID-DVDY1>3.0.CO;2-T)
- Samnegård, U., Hambäck, P.A., Nemomissa, S., Hylander, K., 2014. Dominance of the semi-wild honeybee as coffee pollinator across a gradient of shade-tree structure in Ethiopia. *J. Trop. Ecol.* 30, 401–408. <https://doi.org/10.1017/s0266467414000327>
- Schmitt, C.B., Senbeta, F., Denich, M., Preisinger, H., Boehmer, H.J., 2010. Wild coffee management and plant diversity in the montane rainforest of southwestern Ethiopia. *Afr. J. Ecol.* 48, 78–86. <https://doi.org/10.1111/j.1365-2028.2009.01084.x>
- Senbeta, F., Denich, M., 2006. Effects of wild coffee management on species diversity in the Afromontane rainforests of Ethiopia. *For. Ecol. Manage.* 232, 68–74. <https://doi.org/10.1016/j.foreco.2006.05.064>
- Sist, P., Mazzei, L., Blanc, L., Rutishauser, E., 2014. Large trees as key elements of carbon storage

- and dynamics after selective logging in the Eastern Amazon. *For. Ecol. Manage.* 318, 103–109. <https://doi.org/10.1016/j.foreco.2014.01.005>
- Stephenson, N.L., Das, A.J., Condit, R., Russo, S.E., Baker, P.J., Beckman, N.G., Coomes, D.A., Lines, E.R., Morris, W.K., Rüger, N., Álvarez, E., Blundo, C., Bunyavejchewin, S., Chuyong, G., Davies, S.J., Duque, Á., Ewango, C.N., Flores, O., Franklin, J.F., Grau, H.R., Hao, Z., Harmon, M.E., Hubbell, S.P., Kenfack, D., Lin, Y., Makana, J.-R., Malizia, A., Malizia, L.R., Pabst, R.J., Pongpattananurak, N., Su, S.-H., Sun, I.-F., Tan, S., Thomas, D., van Mantgem, P.J., Wang, X., Wiser, S.K., Zavala, M.A., 2014. Rate of tree carbon accumulation increases continuously with tree size. *Nature* 507, 90–93. <https://doi.org/10.1038/nature12914>
- Sullivan, M.J.P., Talbot, J., Lewis, S.L., Phillips, O.L., Qie, L., Begne, S.K., Chave, J., Cuni-Sanchez, A., Hubau, W., Lopez-Gonzalez, G., Miles, L., Monteagudo-Mendoza, A., Sonké, B., Sunderland, T., ter Steege, H., White, L.J.T., Affum-Baffoe, K., Aiba, S., de Almeida, E.C., de Oliveira, E.A., Alvarez-Loayza, P., Dávila, E.Á., Andrade, A., Aragão, L.E.O.C., Ashton, P., Aymard, C., G.A., Baker, T.R., Balinga, M., Banin, L.F., Baraloto, C., Bastin, J.-F., Berry, N., Bogaert, J., Bonal, D., Bongers, F., Brien, R., Camargo, J.L.C., Cerón, C., Moscoso, V.C., Chezeaux, E., Clark, C.J., Pacheco, Á.C., Comiskey, J.A., Valverde, F.C., Coronado, E.N.H., Dargie, G., Davies, S.J., De Canniere, C., Djuikouo, K., M.N., Doucet, J.-L., Erwin, T.L., Espejo, J.S., Ewango, C.E.N., Fauset, S., Feldpausch, T.R., Herrera, R., Gilpin, M., Gloor, E., Hall, J.S., Harris, D.J., Hart, T.B., Kartawinata, K., Kho, L.K., Kitayama, K., Laurance, S.G.W., Laurance, W.F., Leal, M.E., Lovejoy, T., Lovett, J.C., Lukasu, F.M., Makana, J.-R., Malhi, Y., Maracahipes, L., Marimon, B.S., Junior, B.H.M., Marshall, A.R., Morandi, P.S., Mukendi, J.T., Mukinzi, J., Nilus, R., Vargas, P.N., Camacho, N.C.P., Pardo, G., Peña-Claros, M., Pétronelli, P., Pickavance, G.C., Poulsen, A.D., Poulsen, J.R., Primack, R.B., Priyadi, H., Quesada, C.A., Reitsma, J., Réjou-Méchain, M., Restrepo, Z., Rutishauser, E., Salim, K.A., Salomão, R.P., Samsodin, I., Sheil, D., Sierra, R., Silveira, M., Slik, J.W.F., Steel, L., Taedoumg, H., Tan, S., Terborgh, J.W., Thomas, S.C., Toledo, M., Umunay, P.M., Gamarra, L.V., Vieira, I.C.G., Vos, V.A., Wang, O., Willcock, S., Zemagho, L., 2017. Diversity and carbon storage across the tropical forest biome. *Sci. Rep.* 7, 39102. <https://doi.org/10.1038/srep39102>
- Tadesse, G., Zavaleta, E., Shennan, C., 2014a. Coffee landscapes as refugia for native woody biodiversity as forest loss continues in southwest Ethiopia. *Biol. Conserv.* 169, 384–391. <https://doi.org/10.1016/j.biocon.2013.11.034>
- Tadesse, G., Zavaleta, E., Shennan, C., FitzSimmons, M., 2014b. Policy and demographic factors shape deforestation patterns and socio-ecological processes in southwest Ethiopian coffee agroecosystems. *Appl. Geogr.* 54, 149–159. <https://doi.org/10.1016/j.apgeog.2014.08.001>
- Teketay, D., Senbeta, F., Maclachlan, M., Bekele, M., Barklund, P., 2010. Edible wild plants in Ethiopia. Addis Ababa University Press, Addis Ababa.
- UNEP, 2016. The contribution of forests to national income in Ethiopia and linkages with REDD+. United Nations Environment Programme (UNEP), United Nations Environment Programme. Nairobi (Kenya).
- UNEP WCMC, 2002. World atlas of biodiversity: Earth's living resources in the 21st century. Prepared by the United Nations Environment Programme (UNEP) World Conservation Monitoring Centre (WCMC). University of California Press, Berkeley (USA).
- Vaast, P., Bertrand, B., Perriot, J.J., Guyot, B., Génard, M., 2006. Fruit thinning and shade improve bean characteristics and beverage quality of coffee (*Coffea arabica* L.) under optimal conditions. *J. Sci. Food Agric.* 86, 197–204. <https://doi.org/10.1002/jsfa.2338>
- Vanderhaegen, K., Teopista, K., Dekoninck, W., Jocqué, R., Muys, B., 2018. Do private coffee standards 'walk the talk' in improving socio-economic and environmental sustainability? *Glob. Environ. Chang.* 51, 1–9. <https://doi.org/10.1016/j.gloenvcha.2018.04.014>
- Vanderhaegen, K., Verbist, B., Hundera, K., Muys, B., 2015. REALU vs. REDD+: Carbon and biodiversity in the Afromontane landscapes of SW Ethiopia. *For. Ecol. Manage.* 343, 22–33. <https://doi.org/10.1016/j.foreco.2015.01.016>
- Venter, O., 2014. Corridors of carbon and biodiversity. *Nat. Clim. Chang.* 4, 91–92. <https://doi.org/10.1038/nclimate2115>
- Vergara, C.H., Badano, E.I., 2009. Pollinator diversity increases fruit production in Mexican coffee plantations: The importance of rustic management systems. *Agric. Ecosyst. Environ.* 129, 117–

687 123. <https://doi.org/10.1016/j.agee.2008.08.001>
688 Walker, L.R., Wardle, D.A., Bardgett, R.D., Clarkson, B.D., 2010. The use of chronosequences in
689 studies of ecological succession and soil development. *J. Ecol.* 98, 725–736.
690 <https://doi.org/10.1111/j.1365-2745.2010.01664.x>
691 Wickham, H., 2016. *ggplot2: Elegant graphics for data analysis*, 2nd ed. Springer-Verlag, New York.
692 Zewde, B., 2002. *A history of modern Ethiopia 1855-1991*, 2nd ed. Addis Ababa University Printing
693 Press.
694
695

Figure. 1. Location of the 32 study plots in selected moist Afromontane forest fragments in Mana district, situated between the towns of Jimma and Agaro (Jimma zone, Oromia region, Southwest-Ethiopia). Dotted lines represent asphalt road.

Figure 2. Estimated marginal means comparing forest diversity and structure in 32 plots within moist Afromontane forest remnants in 2009 and 2017. **(A)** Hill's N_0 , Hill's N_1 , and Hill's N_2 in effective number of tree and shrub species; **(B)** Density in number of trees and shrubs ha^{-1} ; **(C)** Basal area in $\text{m}^2 \text{ha}^{-1}$; **(D)** Overall and dominant tree height in m. Boxes represent the 95% confidence interval, horizontal lines within the boxes represent EMM values. Codes for significant differences between the two years: $\cdot p = 0.1 - 0.05$, $* p = 0.05 - 0.01$, $** p = 0.01 - 0.001$, $*** p \leq 0.001$

Figure 3. Non-metric multidimensional scaling (NMDS) ordination of 32 plots surveyed in 2009 (●) and the same 32 plots surveyed in 2017 (▲). The ordination shows the vegetation species community composition for both survey years, plots located close to each other share a similar community composition of woody species (DBH $\geq$ 5 cm). Size of the plotted symbols correspond with surface area (ha) of the forest fragment in which the plots were located. **(A)** Confidence ellipses based on the standard deviations of the points for both survey years are presented. The symbols of certain plots overlap, therefore all plots are individually indicated in Fig. S2A. **(B)** Indication of woody species in the ordination. The shift in community composition per plot between survey years is visualized in Fig. S2C, and species names are listed in Table S1. NMDS ordinations of the third axis are presented in Fig. S3.

Table 1. Estimated marginal means (EMM) and standard errors (SE), differences between both years (Δ), test statistics, and p -values summarized for the evaluated forest diversity and structure elements.

	2009 (n = 32) EMM ($\pm$ SE)	2017 (n = 32) EMM ($\pm$ SE)	Δ (%)	Test statistic	p
<i>Woody vegetation diversity</i>					
Hill's N_0	3.30 ($\pm$ 0.37)	2.53 ($\pm$ 0.32)	-0.77 (-23.4%)	$\chi^2 = 3.47$	0.063
Hill's N_1	1.85 ($\pm$ 0.25)	1.59 ($\pm$ 0.19)	-0.26 (-14.1%)	$\chi^2 = 13.22$	< 0.001
Hill's N_2	1.67 ($\pm$ 0.21)	1.44 ($\pm$ 0.16)	-0.23 (-13.8%)	$\chi^2 = 16.04$	< 0.001
<i>Forest structure</i>					
Basal area	18.53 ($\pm$ 2.46)	18.14 ($\pm$ 2.39)	-0.39 (-2.1%)	$\chi^2 = 0.03$	0.866
Density	191.84 ($\pm$ 19.09)	132.72 ($\pm$ 13.30)	-59.12 (-30.8%)	$z = -3.39$	< 0.001
Tree height	10.99 ($\pm$ 0.68)	12.22 ($\pm$ 0.83)	1.23 (+11.2%)	$\chi^2 = 6.79$	0.009
Dominant tree height	13.81 ($\pm$ 0.83)	13.66 ($\pm$ 0.81)	-0.15 (-1.1%)	$\chi^2 = 0.93$	0.761

A

B

A

B

C

NMDS2

NMDS1

A **B** **C** **D** **E** **F**

25-12-2007

Yabo

Google Earth

Image © 2019 CNES / Airbus

1 km

N

27-11-2017

Yabo

Google Earth

Image © 2019 CNES / Airbus

1 km

Rapid diversity and structure degradation over time through continued coffee cultivation in remnant Ethiopian Afromontane forests

Supplementary Figures and Tables

Figure S1. Species accumulation curves presenting the cumulative species richness of woody vegetation ($\text{DBH} \geq 5 \text{ cm}$) in function of the number of sampled plots. In 2009, 32 plots were sampled and a total of 29 species was recorded. In 2017, the same 32 plots were sampled and a total of 20 species was recorded.

Figure S2. Non-metric multidimensional scaling (NMDS) ordination of 32 plots monitored in 2009 (1-32, ●) and the same plots monitored in 2017 (33-64, ▲). The ordination shows the vegetation species community composition for both monitoring years, plots located close to each other share a similar community composition of woody species (DBH $\geq$ 5cm). **(A)** Indication of all sample plots in the ordination. **(B)** Indication of all species in the ordination. **(C)** Arrows indicate the shift in community composition of each plot from 2009 to 2017.

Figure S3. Non-metric multidimensional scaling (NMDS) ordination of 32 plots surveyed in 2009 (●) and the same 32 plots surveyed in 2017 (▲). The ordination shows the vegetation species community composition for both survey years, plots located close to each other share a similar community composition of woody species (DBH $\geq$ 5 cm). Size of the plotted symbols correspond with surface area (ha) of the forest fragment in which the plots were located. (A-C) Confidence ellipses based on the standard deviations of the points for both survey years are presented. A different ordination is presented for each axis combination. (D-F) Indication of woody species in the ordinations. Different ordinations are presented for each axis combination.

Figure S4. Screenshot of Google Earth images, representing the Afromontane forest remnants in our study landscape (Mana district, Jimma zone, Southwest-Ethiopia) at time points that are as close as possible to the actual survey dates (only a limited number of time points options were available). Top image dates from 25/12/2007, bottom image date from 27/11/2017.

Table S1. Species list and ecological information of recorded trees and shrubs in 32 study plots in moist Afromontane forest remnants in SW Ethiopia. Abundances are presented per monitoring year.

Species name	Family	Distribution in Ethiopia	Successional stage	Abundance	
				2009 (n = 32)	2017 (n = 32)
<i>Acacia abyssinica</i> et al.	Fabaceae	native	early *	6	6
<i>Albizia gummifera</i> / <i>schimperiana</i> .	Fabaceae	native	early *	89	72
<i>Allophylus abyssinicus</i> (HOCHST.) RADLK.	Sapindaceae	native	late °	6	2
<i>Apodytes dimidiata</i> E. MEY. EX ARN.	Icacinaceae	native	late *	0	1
<i>Bersama abyssinica</i> FRESEN.	Melanthaceae	native	early *	15	7
<i>Bucea antidysenterica</i> J. F. MILL.	Simaroubaceae	native	early °	2	0
<i>Celtis africana</i> BURM.F.	Cannabaceae	native	early °	2	1
<i>Clausena anisata</i> (WILLD.) HOOK. F. EX BENTH.	Rutaceae	native	(?)	1	0
<i>Cordia africana</i> LAM.	Boraginaceae	native	early *	8	7
<i>Croton macrostachyus</i> HOCHST. EX DELILE	Euphorbiaceae	native	early *	41	41
<i>Dracaena steudneri</i> ENGL.	Agavaceae	native	(?)	0	1
<i>Ehretia cymosa</i> THONN.	Boraginaceae	native	(?)	6	6
<i>Ekebergia capensis</i> SPARRM.	Meliaceae	native	(?)	0	2
<i>Erythrina brucei</i> SCHWEINF.	Fabaceae	endemic	early ◇	1	0
<i>Euphorbia ampliphylla</i> PAX	Euphorbiaceae	native	early ◇	1	0
<i>Ficus sycomorus</i> L.	Moraceae	native	early ◇	2	1
<i>Ficus thonningii</i> BLUME	Moraceae	native	early ◇	2	1
<i>Grevillea robusta</i> A. CUNN. EX R. BR.	Proteaceae	exotic	early ◇	6	0
<i>Ilex mitis</i> (L.) RADLK.	Aquifoliaceae	native	(?)	2	0
<i>Macaranga capensis</i> (BAILL.) SIM	Euphorbiaceae	native	early °	2	0
<i>Maesa lanceolata</i> FORSSK.	Myrsinaceae	native	early ◇	8	7
<i>Millettia ferruginea</i> (HOCHST.) BAKER	Fabaceae	endemic	early *	27	13
<i>Pouteria adolfi-friedericii</i> (ENGL.) A.MEEUSE	Sapotaceae	native	late °	4	1
<i>Premna schimperi</i> ENGL.	Verbenaceae	native	early ◇	1	0
<i>Psidium guajava</i> L.	Myrtaceae	exotic	early ◇	1	0
<i>Psychotria orophila</i> E.M.A.PETTIT	Rubiaceae	native	(?)	5	0
<i>Sapium ellipticum</i> (HOCHST.) PAX	Euphorbiaceae	native	early *	2	1
<i>Schefflera abyssinica</i> (HOCHST. EX A.RICH.) HARMS	Araliaceae	native	(?)	1	1
<i>Sesbania sesban</i> (L.) MERR.	Fabaceae	native	early ◇	1	0
<i>Syzygium guineense</i> (WILLD.) DC.	Myrtaceae	native	(?)	15	7
Unidentified species	-	-	-	1	0
<i>Vernonia auriculifera</i> HIERN	Asteraceae	native	early °	5	3
Total				263	181

* Fichtl, R., Admasu, A., 1994. Honeybee flora of Ethiopia, 1st ed. Margraf Verlag, Weikersheim (Germany).

° PROTA4U. Plant Resources of Tropical Africa: web database. <https://www.prota4u.org/database/> (accessed 11.01.19).

◇ Fern, K., 2014. Tropical Plants Database. <http://www.tropical.theferns.info> (accessed 11.01.19).

Table S2. Occurrences of woody vegetation species (DBH $\geq$ 5 cm) per plot for the 2009-survey. Full names for the species can be found in Table 1.

2009	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15	P16	P17	P18	P19	P20	P21	P22	P23	P24	P25	P26	P27	P28	P29	P30	P31	P32	
Aca.sp	0	0	4	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	
Alb.sp	1	0	10	1	4	3	4	2	2	1	4	2	8	3	4	2	0	0	1	3	7	1	1	0	6	4	0	0	0	9	1	5	
All.ab	0	0	2	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Apo.di	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Ber.ab	0	0	2	0	0	4	0	0	2	1	1	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	
Bru.an	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Cel.af	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Cla.an	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Cor.af	0	1	0	2	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	
Cro.ma	2	4	0	0	0	1	0	2	0	3	2	2	0	6	0	1	3	1	1	0	0	3	0	2	0	0	2	0	3	0	3	0	0
Dra.st	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Ehr.cy	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Eke.ca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Ery.br	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Eup.am	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Fic.sy	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
Fic.th	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Gre.ro	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Gut.un	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	
Ile.mi	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Mac.ca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	
Mae.la	2	0	0	0	0	0	0	0	0	0	2	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Mil.fe	2	0	0	0	3	0	3	0	3	0	2	0	2	1	1	0	0	4	1	0	0	0	2	3	0	0	0	0	0	0	0	0	
Pou.ad	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	
Pre.sc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	
Psi.gu	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Psy.or	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Sap.el	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Sch.ab	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	
Ses.se	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Syz.gu	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	1	0	0	3	6	0	0	0	0	
Ver.au	0	0	0	0	0	0	0	0	0	1	0	0	0	3	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	

Table S3. Occurrences of woody vegetation species ($\text{DBH} \geq 5 \text{ cm}$) per plot for the 2017-survey. Plot 33 (P33) of the 2017-survey corresponds to plot 1 (P1) of the 2009-survey. Full names for the species can be found in Table 1.

2017	P33	P34	P35	P36	P37	P38	P39	P40	P41	P42	P43	P44	P45	P46	P47	P48	P49	P50	P51	P52	P53	P54	P55	P56	P57	P58	P59	P60	P61	P62	P63	P64
Aca.sp	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alb.sp	0	1	1	1	0	0	0	1	1	6	1	4	3	2	5	3	1	1	1	2	5	6	1	3	5	6	0	0	5	5	1	1
All.ab	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Apo.di	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ber.ab	0	0	0	2	0	2	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bru.an	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cel.af	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cla.an	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cor.af	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	1	0	0	0
Cro.ma	6	4	4	1	3	0	1	1	2	0	0	0	0	1	1	0	3	1	0	1	0	1	2	0	0	0	0	7	1	0	1	0
Dra.st	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ehr.cy	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eke.ca	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ery.br	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eup.am	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fic.sy	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fic.th	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gre.ro	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gut.un	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ile.mi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mac.ca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mae.la	0	0	0	0	0	0	0	0	0	4	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Mil.fe	1	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	2	0	0	0	1	0	0	0	3	1	1	1	0	0	0
Pou.ad	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pre.sc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psi.gu	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psy.or	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sap.el	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sch.ab	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ses.se	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Syz.gu	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	2	1	0	0	0	0
Ver.au	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0

Table S4. Full models, evaluating differences in forest structure between the two monitoring years (2009, n = 32; and 2017, n = 32). Test statistic, degrees of freedom (df), and *p*-value are presented for each factor, along with the probability distribution and link function by which each dependent variable was modelled (Family function).

Forest structure	Test statistic	df	<i>p</i>	Family function
<i>Hill's N0</i>				
Year	$\chi^2 = 3.45$	1	0.063	Poisson log link
Fragment size	$\chi^2 = 0.31$	1	0.577	
Fragment size*Year	$\chi^2 = 0.18$	1	0.673	
<i>Hill's N1</i>				
Year	$\chi^2 = 14.07$	1	< 0.001	Gamma inverse link
Fragment size	$\chi^2 = 0.40$	1	0.529	
Fragment size*Year	$\chi^2 = 0.91$	1	0.340	
<i>Hill's N2</i>				
Year	$\chi^2 = 16.72$	1	< 0.001	Gamma inverse link
Fragment size	$\chi^2 = 0.51$	1	0.474	
Fragment size*Year	$\chi^2 = 0.94$	1	0.333	
<i>Plot basal area</i>				
Year	$\chi^2 = 0.02$	1	0.880	Gamma inverse link
Fragment size	$\chi^2 = 4.98$	1	0.026	
Fragment size*Year	$\chi^2 = 0.41$	1	0.523	
<i>Density</i>				
Year	<i>z</i> = -2.02	1	0.043	Negative binomial log link
Fragment size	<i>z</i> = 1.61	1	0.108	
Fragment size*Year	<i>z</i> = -0.91	1	0.365	
<i>Tree height</i>				
Year	$\chi^2 = 6.66$	1	0.010	Gamma inverse link
Fragment size	$\chi^2 = 0.53$	1	0.467	
Fragment size*Year	$\chi^2 = 0.38$	1	0.540	
<i>Dominant tree height</i>				
Year	$\chi^2 = 0.09$	1	0.770	Gamma inverse link
Fragment size	$\chi^2 = 2.25$	1	0.134	
Fragment size*Year	$\chi^2 = 0.18$	1	0.673	

Table S5. Reduced models evaluating differences in forest structure between the two monitoring years (2009, n = 32; and 2017, n = 32). Model estimates (β) with standard errors (SE), test statistic, degrees of freedom (df), and p -value are presented for each factor. The probability distribution and link function by which each dependent variable was modelled is presented (Family function).

Forest structure		β ($\pm$ SE)	Test statistic	df	p	Family function
<i>Hill's N0</i>						
Year	2009:	1.19 ($\pm$ 0.11)	$\chi^2 = 3.47$	1	0.063	Poisson log link
	2017:	0.93 ($\pm$ 0.14)				
<i>Hill's N1</i>						
Year	2009:	0.54 ($\pm$ 0.07)	$\chi^2 = 13.22$	1	< 0.001	Gamma inverse link
	2017:	0.63 ($\pm$ 0.02)				
<i>Hill's N2</i>						
Year	2009:	0.60 ($\pm$ 0.07)	$\chi^2 = 16.04$	1	< 0.001	Gamma inverse link
	2017:	0.69 ($\pm$ 0.02)				
<i>Plot basal area</i>						
Year	2009:	0.06 ($\pm$ 0.01)	$\chi^2 = 0.03$	1	0.866	Gamma inverse link
	2017:	0.06 ($\pm$ 0.01)				
Fragment size		- 0.00 ($\pm$ 0.00)	$\chi^2 = 1.39$	1	0.238	
<i>Density</i>						
Year	2009:	5.26 ($\pm$ 0.10)	$z = -3.39$	1	< 0.001	Negative binomial log link
	2017:	4.89 ($\pm$ 0.11)				
<i>Tree height</i>						
Year	2009:	0.09 ($\pm$ 0.01)	$\chi^2 = 6.79$	1	0.009	Gamma inverse link
	2017:	0.08 ($\pm$ 0.00)				
<i>Dominant tree height</i>						
Year	2009:	0.08 ($\pm$ 0.00)	$\chi^2 = 0.93$	1	0.761	Gamma inverse link
	2017:	0.08 ($\pm$ 0.00)				
Fragment size		-0.00 ($\pm$ 0.00)	$\chi^2 = 2.32$	1	0.127	