Management intensity and landscape configuration affect the potential for woody plant regeneration in coffee agroforestry

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\textbf{ARTICLE INFO}

\textbf{Keywords:} Biodiversity, Conservation, Forest fragmentation, Microclimate, Seed dispersal

\textbf{ABSTRACT}

With the current deforestation rates in tropical ecosystems, optimizing biodiversity in managed systems has become fundamental for conservation. Agroforestry has been suggested to conserve biodiversity and buffer deforestation rates, while also sustaining local livelihoods. While many studies have focused on the relation between local management intensity and biodiversity, processes at the landscape scale are often overlooked and remain a knowledge gap.

In this study we identified drivers behind woody plant regeneration in coffee agroforestry on both local and landscape scale. We used univariate-, multivariate- and structural equation models to relate seedling species richness, diversity, density, community composition and height to local management intensity and location in the landscape of 60 coffee agroforestry sites in southwestern Ethiopia.

Local management intensity, which simplifies and reduces canopy cover, negatively impacted species richness, diversity and density, presumably due to altered microclimatic conditions and a reduction in local seed sources. Seedling height was also reduced by management intensity, including slashing frequency and canopy cover. On the landscape scale, species richness and diversity of seedlings was higher at sites adjacent to continuous forests where seed sources are abundant, and declined with distance to the forest. In particular, late successional species were negatively affected, whereas common shade tree species and pioneers occurred as seedlings throughout the landscape and in more managed systems. This suggests that dispersal limitation is detrimental for the regeneration of late successional species, especially in agroforestry systems where the standing woody plant diversity is largely reduced.

Our results indicate that natural regeneration of woody plants still occurs in coffee agroforestry systems, primarily when the canopy structure is dense and diverse and/or when sites are located nearby continuous forests. Management intensification and deforestation will limit the potential for many woody plant species to regenerate in coffee agroforestry sites, by altering the local microclimate, reducing local seed sources and disrupting seed dispersal from the surrounding landscape. This will likely result in a positive feedback loop, as a reduction in woody plant regeneration reduces future seed sources. We therefore stress that both a local and a landscape perspective should be incorporated in conservation and restoration approaches.

\textbf{1. Introduction}

Deforestation is one of the major threats to tropical forests and their associated biodiversity, with agricultural expansion being the primary cause (Taubert et al., 2018). Worldwide, tropical forests are converted into mosaic landscapes where forest fragments are embedded in strongly managed areas such as annual crop fields and urbanized areas (Norris et al., 2010; Pütz et al., 2011) and remnants of continuous forest are often largely intertwined with the livelihoods of the local population (Norris et al., 2010). This puts forest biodiversity at large risk (Norris et al., 2010; Pütz et al., 2011; Laurance et al., 2011) and strategies to maintain or restore biodiversity in a human dominated landscape are fundamental topics in conservation biology. Agroforestry is the cultivation of agricultural crops, such as cacao (Theobroma cacao) or coffee...
dispersal ability (Cordeiro and Howe, 2001). However, the dispersal of species such as birds, bats and primates, which have lower densities in the source and increases with surrounding forest area (Cordeiro and Howe, 2007a; Bisseleu et al., 2009). With the current deforestation rates, there is a need to determine the potential for biodiversity conservation in agroforestry systems. One of the major steps is to identify processes that drive regeneration of forest vegetation in agroforestry systems. While the majority of the studies have focused on the effects of local conditions on tree diversity in agroforestry systems, the landscape scale is often neglected, even though it may play a key role in maintaining local diversity. Studies on the local and spatial drivers of tree regeneration in agroforestry are particularly under-represented (but see Tadesse et al., 2014a; and Hundera et al., 2013 and 2015 for studies on local drivers). However, evaluating the diversity of adult trees may not provide an accurate estimate of biodiversity that could be sustained in the long run, as adult vegetation might still be present in an area where they cannot reproduce or recruit, also known as extinction debt (Norris et al., 2010; Hylander and Nemomissa, 2017).

Local conditions in agroforestry are largely determined by management intensity. Many studies have pointed out that intensive management reduces the woody plant biodiversity (e.g. Schmitt et al., 2010; Senbeta and Denich, 2006; Hundera et al., 2013; Valencia et al., 2016; Geeraert et al., 2019) and reduces the potential for the regeneration of trees (Tadesse et al., 2014a). Management practices frequently include selective thinning of the canopy to achieve favorable light conditions and removal of the understory vegetation to diminish competition with the crop (Schmitt et al., 2010; Aerts et al., 2011). This includes (selective) removal of tree seedlings and thus interferes with the natural regeneration process (Hundera et al., 2013). The canopy in highly managed agroforestry systems is often dominated by only a few common tree species, which largely simplifies the diversity in local seed sources (Aerts et al., 2011; Valencia et al., 2016). Hundera et al. (2015) found the regeneration of late successional trees in agroforestry to be lacking due to the absence or low abundance of adults in the canopy, while common shade tree species regenerated successfully in the absence of slashing (Hundera et al., 2015). Another important implication for tree regeneration is the microclimatic change (including higher light radiation, temperatures and wind speeds) related to reduced canopy cover (Beer et al., 1997; Frey et al., 2016; Kovacs et al., 2017). Especially late successional species are largely disfavored by reduced canopy cover, while the regeneration of pioneer species, that can thrive with disturbance and light, is facilitated.

The simplified canopy structures in agroforestry are often dominated by common shade trees and pioneers. Hence, colonization of forest specialist trees relies on dispersal from adjacent forests, indicating that location in the landscape might be a key factor in determining regeneration potential. However, processes on landscape scale related to the regeneration of trees in agroforestry systems remain a gap in our knowledge. We know from other systems that the disruption of seed dispersal is a major constraint for biodiversity conservation (Mendonça-Lima de et al., 2014; Tellia et al., 2015), indicating that such processes should be also included in biodiversity studies related to agroforestry. Generally, dispersal decreases with distance from the source and increases with surrounding forest area (Cordeiro and Howe, 2001; Melo et al., 2007). Wind dispersed seeds are less limited in their dispersal ability (Cordeiro and Howe, 2001). However, the dispersal of seeds in the tropics relies mainly on frugivorous animals (Willson et al., 1989), such as birds, bats and primates, which have lower densities in fragmented landscapes as compared to continuous forests (Cordeiro and Howe, 2001; Bovo et al., 2018).

In this study we examined processes on the local and landscape scale that drive tree regeneration in coffee agroforestry sites in southwestern Ethiopia. Coffea arabica, which is a native understory shrub of the Afromontane forests of Ethiopia, is a widely cultivated crop that provides an important source of income for local communities (Schmitt et al., 2010; Jena et al., 2012). Major parts of the Afromontane forests have been replaced by a mosaic of coffee agricultural patches and open crop fields and a further increase in deforestation and management intensity puts its biodiversity at great risk (Tadesse et al., 2014b; Geeraert et al., 2019). We selected 60 coffee agroforestry sites in southwestern Ethiopia that covered a large variation in management intensity, as well as in the proportion of the surrounding landscape that was covered by forests. We hypothesized that the species richness, diversity and density of seedlings decline with management intensity and increase in sites close to continuous forest or with high tree cover surrounding the sites. We also hypothesized that seedling community composition is affected by both local and landscape processes and that seedling height is negatively affected by management intensity.

2. Methods

2.1. Study area

We conducted our study in the Gomma and Gera districts (7° 48′ –7° 53′ N and 36° 33′–36° 36′ E) in southwestern Ethiopia (Fig. 1a). The landscape used to be covered by moist Afromontane forest, dominated by species such as Syzygium guineense, Sapinum ellipticum, and Olea welwitchii (Friis et al., 2010), but is nowadays characterized by a mosaic of coffee agroforestry and annual crop fields (Ango et al., 2014). The last primary forests are disappearing at a high rate (Tadesse et al., 2014b; Rodrigues et al., 2018), putting its associated biodiversity at great risk. Coffee agroforestry comprises a major part of the secondary forests in the study area, dominated by the common shade tree species Albizia gummifera, Albizia schimperiana, Cordia africana, Croton macrostachyus, and Millettia ferruginea (Aerts et al., 2011). The elevation in our study area ranges from 1500 to 2200 m above sea level. The mean annual temperature is 20 °C and the annual rainfall ranges between 1500 and 2000 mm, with the rainy season occurring from May to September (Friis et al., 1982; Denu et al., 2016).

Our study included 60 agroforestry sites distributed across the landscape, comprising an area of approximately 50 by 50 km (Fig. 1B) (Zewdie et al., 2020). These included 51 smallholder farms and 3 different commercial plantations. Some sites were close to remnants of continuous Afromontane forest or surrounded by several smaller patches of primary or secondary forests, whereas other sites were embedded in an open agricultural landscape with annual crops. Remnants of continuous Afromontane forest are located to both the west and to the east (Fig. 1B). The sites represented a gradient of management intensity that ranged from little interference, leaving a dense and diverse canopy cover, to heavily modified sites that used intensive management to increase coffee yield (Fig. 1D).

2.2. Data collection

2.2.1. Seedling inventory

Seedling inventory was conducted in July and August 2018. At all 60 sites, a 30 × 30 m area was established, which was subdivided into 9 plots of 10 × 10 m by marking the coffee shrubs in the intersection of these (Fig. 1C). We inventoried seedlings within 2 × 2 m subplots in the centre of the 9 plots, which were temporarily marked with a rope during fieldwork. At 45 sites we inventoried all 9 subplots but at 15 sites we only completed the inventory of 5–8 subplots. For simplicity, seedlings were in this study defined as all woody species shorter than 50 cm, but the majority were small (<20 cm). All seedlings in the 2 × 2 m subplots...
were identified to species level, counted and measured. Species identification was primarily conducted in the field with the help of a field key to Ethiopian trees (Chaffey, 1890), the Flora of Ethiopia (1989–2006), Flora of Ethiopia and Eritrea, 1989 Flora of Ethiopia (1989–2006), as well as the botanical knowledge of local farmers. Unknown specimens were collected for later identification at the National Herbarium of Ethiopia, Addis Ababa. As small Calpurnia aurea seedlings were difficult to distinguish from other Fabaceae species (including herbs and other shrubs), we omitted all individuals smaller than 20 cm from the dataset before analyses, potentially leading to an underestimation of the frequency of this species. Seedling height was measured from the soil to the top of the main stem for each individual. We determined species richness, diversity and density for each 2 × 2 subplot within a site and for each site overall. To allow comparison of species richness between sites, we rarefied species richness down to 5 subplots per site (i.e. the minimum number of subplots recorded in a site) using the R package vegan (Oksanen et al., 2013). We calculated seedling diversity, using the Shannon index from the vegan package, for all subplots within sites and on site-level by taking the average diversity across all 2 × 2 m subplots. Similarly, we calculated seedling abundance for all subplots within sites and calculated seedling density for each site by taking the average abundance of seedlings across all 2 × 2 m subplots. Finally, we calculated the average height for each species per site.

2.2.2. Local variables

Local data included canopy cover, identity of mature trees and shrubs, soil moisture and slashing frequency, and was collected during three different field seasons in 2017 and 2018 (Appendix, Table S1). Canopy cover was calculated with the software ImageJ v. 1.51, based on photos that were taken in a vertical direction above the coffee shrubs using a Nikon Coolpix S2800 camera at 5 locations in each site (Zewdie et al., 2020). Inventory of shade trees and shrubs larger than 1.5 m was conducted in a 50 × 50 m area including the central 9 plots (Zewdie et al., 2020). Based on this we calculated the species richness of adult woody plants at each site. Soil moisture was measured using the SM150 soil moisture kit from Delta-T Devices. A measure of soil moisture was calculated for each site by averaging soil moisture values from 8 locations within the site, with 3 measurements at each location Soil moisture measures were missing from 9 sites. Information about slashing frequency per year was obtained from interview data with farmers from the smallholder systems (Schober, 2018). This data consisted of 4 categories: less than once per year, once per year, twice per year, and more than twice per year. Plantations were not included in the interview data and were later added as a fifth factor level, as these are frequently slashed and sometimes sprayed with herbicides. 5 smallholder farms were missing from this dataset. Additionally, to assess if microclimatic differences within sites drive the regeneration of seedling species richness, we counted the number of shade trees above each 2 × 2 m subplot, identified them to species level and estimated their coverage.

2.2.3. Landscape characteristics

We measured the distance from each site to the nearest continuous
areas of Afromontane moist forest using Google Earth pro v. 7.3.2.5491 (the continuous forests are denoted by a tree symbol in Fig. 1B). Based on knowledge from working in this region for many years, we believe that these continuous forests are structurally diverse and relatively undisturbed compared to the small fragments in the mosaic landscape. We measured the area with tree cover surrounding the 60 sites within a radius 1 km using ArcMAP v. 10.6.1 from ArcGIS Desktop on a layer where we had classified the landscape into forests and non-forests.

### 2.3. Statistical analyses

Statistical analyses were conducted in the software R (version 3.6.1). We conducted piecewise Structural Equation Models (SEM) to investigate the effects of local and landscape variables on seedling species richness, diversity and density in agroforestry sites, using the package PiecewiseSEM (Zeilke, 2016). We simultaneously tested for local and landscape variables in the models, in order to investigate their relative importance on tree regeneration and to test pathways between local and landscape variables that could have indirect effects. We scaled the explanatory variables in order to obtain standardized and thus comparable coefficients. Local variables included canopy cover, identity of mature trees and shrubs, soil moisture and slashing frequency, and landscape variables included log_{10} transformed distance to continuous forest and surrounding area with tree cover within 1 km. The piecewise SEM does not allow for categorical variables. In order to include slashing frequency, we transformed it to a numerical variable from 0 to 4 corresponding to the levels: less than once per year, once per year, twice per year, more than twice per year and plantations respectively. Correlational between the explanatory variables can be found in Appendix, Table S2. First, we created a hypothetical pathway diagram based on our expected relationships between the response and explanatory variables (Fig. 2A). Our initial SEMs were based on these hypothetical relationships, referred to as component equations. We assumed a Poisson distribution for the component equation with species richness of woody plants as response variable (count data) and Gaussian distribution for the other component equations. Seedling density was log_{10}-transformed to meet the assumptions of a linear model. We then eliminated and added pathways based on the directional separation tests, until we found the models with the best fit. The fit of the models was estimated based on the lowest AIC as well as the Fisher’s C statistic and associated p-value of a directional separation test, where the highest p-value indicates the best fitting model (Zielke, 2016). To assess if the seedling community composition was affected by local conditions and location in the landscape, we ran an NMDS ordination on a species-by-site matrix with 2 dimensions, Bray-Curtis dissimilarity index and default settings in the vegan package (Oksanen et al., 2013). To account for the different number of investigated subplots, we used the density of each species (total abundance divided by the number of subplots inventoried) in the species-by-site matrix. We used the envfit-function to evaluate if our explanatory variables were related to the gradients in species composition. To illustrate how individual species were related to these gradients, we plotted the species scores along the two NMDS axes together with our explanatory variables. Due to a rather high stress level for the 2-dimensional NMDS, we also conducted a NMDS with 3 dimensions, which showed the same pattern. We present the results for the 2-dimensional NMDS since it is easier to illustrate. To test for the association between the community composition of adult woody plants and seedlings we conducted a Mantel test, both for the presence-absence matrices and the matrices including density.

To investigate the drivers behind the height of seedlings, seedling height was modeled as a function of the seedling species, distance to continuous forest, surrounding area with tree cover within 1 km, canopy cover, soil moisture during the dry season and slashing frequency. Slashing frequency was included as an ordinal variable from low to high slashing frequencies. Pairwise comparison between slashing frequencies was conducted with a Tukey test using the multcomp package (Hothorn et al., 2008).

Finally, we modeled within-site variation at the subplot level to test if the local canopy structure within sites was important for the regeneration of seedlings. We modeled seedling species richness, diversity and abundance at each 2 × 2 m subplot as a function of the number of shade trees above, including site as a random effect, using a generalized linear model with a Poisson distribution using the package lme4 (Bates et al., 2015). Similarly, we examined if seedling species richness, diversity and abundance differed with the species of shade-tree above by modeling these seedling community descriptors at each subplot as a function of the shade tree species above and their percentage of coverage. We examined the most common shade tree species: C. macrostachyus, Albizia spp. (including A. gummifera and A. schimperiana) and Cordia africana. They are preserved in agroforestry for characteristics favorable for coffee growth, such as canopy structure, suitable litter, or nitrogen fixing properties (Schmitt et al., 2010; Aerts et al., 2011) or simply because they are fast growing pioneer species, which is the case for C. macrostachyus. We also included Ficus spp., which we hypothesized to increase seed rain due to bird attraction. Pairwise comparison between these shade tree species was conducted with a Tukey test using the multcomp package (Hothorn et al., 2008). We used a Poisson distribution for the models on richness and abundance and a Gaussian distribution for the models on diversity. We checked the residual diagnostics, using the DHARMA package for the models with a Poisson distribution, and corrected for slight overdispersion in the seedling abundance models by adding an individual level random effect (Hartig, 2020).

### 3. Results

#### 3.1. Seedling species richness, density and diversity

We recorded a total of 2417 individual seedlings of 52 species belonging to 27 families (Appendix, Table S3). The number of species found as seedling ranged from 1 to 18 per site, with a mean of 6.8 (± 4.1 SD).

Variation in seedling species richness, diversity and density in coffee agroforestry was explained by both local and landscape variables. Species richness and diversity of seedlings was positively related to canopy cover, species richness of adult woody plants and coverage of trees in the surrounding area, and decreased with distance to continuous forest, especially during the first few kilometers (Figs. 2B and C, 3 A-L). Besides the strong direct effects of these local- and landscape variables on seedling species richness, we found indirect effects of distance to continuous forest mediated by canopy cover and adult woody plant species richness (Fig. 2B and C). Seedling density was positively associated with canopy cover, adult woody plant species richness and surrounding area of tree cover (Figs. 2D and 3 M-R). Distance to forest had no direct effect on seedling density, but had, similar to seedling species richness and diversity, indirect effects (Fig. 2D). Slashing frequency did not affect species richness, diversity or density and was eliminated from the final models. Soil moisture was positively affected by canopy cover, but did not affect the seedling community descriptors. Since there were missing values for soil moisture, this variable reduced the fit of the models and was therefore removed from the final models.

#### 3.2. Seedling community composition

Seedling community composition was related to both local conditions (canopy cover and species richness of adult woody plants) and by location in the landscape (distance to continuous forest and surrounding area with tree cover) (Fig. 4). When species scores were plotted along the two NMDS axes, common shade tree species, such as A. schimperiana, C. macrostachyus and A. abyssinica grouped at the opposite end of the gradient compared to late successional species, such as Dracaenaasleystegnei, S. guineense, O. weehwitchii (Fig. 4). Seedlings of common shade tree species were associated with higher management intensity and
Fig. 2. A. The hypothetical model for the structural equation models. Expected mechanisms behind the hypothetical pathways are shown in grey boxes and are further discussed in the discussion. B-D. The results of the structural equation models showing the direct and indirect effects of landscape and local variables on seedling species richness (B), diversity (C), and density (D). Red arrows indicate negative effects on species richness and black positive effects. Standardized coefficients are given for each relationship and significance is indicated as follows: **P < 0.01, *P < 0.05, .P < 0.1. The Fisher’s C, p-value and AIC (all measures for the fit of the model) are reported on the bottom right for each SEM. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).
further away from continuous forests in the NMDS, whereas late successional species were associated with higher levels of canopy cover and woody plant diversity and higher levels of surrounding forest area (Fig. 4).

A Mantel test showed that seedling community composition was correlated with the community composition of adult woody plants when tested using presence-absence data ($r = 0.39$, $p < 0.001$). However, when variation in density was included, there was no correlation ($r = 0.017$, $p = 0.36$).

### 3.3. Seedling height

Seedling height was positively related to canopy cover (estimate $0.04$, $p = 0.009$). Seedlings were slightly shorter in commercial plantations as compared to smallholder farms (-0.28, $p < 0.001$; -0.18, $p = 0.01$; -0.22, $p = 0.009$ for smallholder farms with slashing frequency 1, 2 or more than 2 respectively).
3.4. Seedling species richness, diversity and abundance within sites

In line with the results of the relationship between the seedling descriptors and local variables between sites, variation in the seedling community descriptors within sites was positively related to canopy cover, measured as the number of shade trees right above (Appendix, Table S4). There was no difference in overall seedling species richness and diversity under different common shade tree species (species richness $p = 0.33$, Fig. 5; diversity $p = 0.13$; abundance $p = 0.052$), but the absence of any shade tree right above resulted in lower woody plant regeneration (species richness $p < 0.001$, Fig. 5; diversity $p = 0.001$; abundance $p < 0.001$). The pairwise differences between the different shade tree species or no species at all can be found in Appendix Table S4.

4. Discussion

The objective of our study was to identify the local and spatial drivers of tree regeneration in coffee agroforestry systems. Variation in local conditions are tightly linked to management practices in coffee agroforestry systems. In line with previous studies, we found that management intensity largely decreased tree regeneration in agroforestry. According to our hypothesis, we found that also location in the landscape explained variation in the seedling community. The regeneration of many species (especially late successional species) are dependent on dispersal from distant sources, as woody plant diversity in agroforestry is largely reduced by intense management. In line with this, we found a higher number of woody plant species regenerating in locations in closer proximity to continuous forests.

4.1. Local processes

Following our expectations, a reduction and simplification of the canopy was associated with lower levels of woody plant regeneration in coffee agroforestry. Management practices include selective thinning of the canopy in order to achieve light conditions for optimized coffee yield. When canopy cover is reduced, the survival of seeds and seedlings might be limited due to exposure to more extreme temperatures, solar radiation and desiccation (Beer et al., 1998; Frey et al., 2016). These altered local microclimatic conditions had a large negative impact on regeneration of woody plants in our study, as is seen by the lower species richness, diversity and density in more open sites. In addition to determining microclimatic conditions in the understory, the canopy provides a habitat for arboreal frugivorous animals and increased local seed rain could be an alternative or complementary explanation for the increase in the seedling community descriptors in sites with a denser canopy. A dense and more diverse canopy has been shown to attract a higher species richness of animals, in particular birds and bats (e.g. Harvey et al., 2006), and strong clustering of seeds beneath the canopy of a tree favorable for roosting and perching by animals has been observed (Telilla et al., 2015). The decline in seedling species richness, diversity and density under reduced canopy cover was not only revealed by comparing different sites, but also when assessing variation in canopy cover within a site, strengthening the conclusion that canopy cover itself is an important driver of tree regeneration. We did not find a difference in seedling species richness in relation to the shade tree species above, despite our hypothesis that some trees would facilitate tree regeneration by attracting frugivores (e.g. Ficus) or enhancing local nitrogen supplies (the nitrogen fixing species: Acacia and Albizzia).

After establishment in a coffee patch, slashing of the understory forms a major barrier for survival for seedlings and has often been implied as one of the largest limitations for tree regeneration in coffee systems (Tesfaye et al., 2002; Aerts et al., 2011; Hundera et al., 2013). Farmers slash the understory vegetation, including emerging trees, to decrease competition with coffee shrubs for water and nutrients. If emerging seedlings do develop into adult trees or shrubs, they are often removed when they start to directly compete with coffee shrubs in the same canopy layer (Senbeta and Denich, 2006; Kumsa et al., 2016). Surprisingly, we did not find effects of slashing frequency on seedling species richness, diversity or density in our study. This might be due to a lack of control sites where slashing was entirely absent. However, we found that seedling height was lower in plantations where besides regularly slashing also herbicides are sometimes applied, which supports the hypothesis that management intensity is a strong filter between the seedling stage and adult trees. Yet, some seedlings/saplings survived the slashing and continued to grow new shoots from the cut stems (personal observation).

4.2. Landscape configuration

The results of our study indicate that the regeneration of woody species is highly dependent on local seed sources. First, we found a correlation between the seedling and adult woody plant community composition for presence/absence, even if there were large differences in which species were over- or under-represented as seedlings in relation to their abundances in the canopy. Second, we showed that sites with a more simplified canopy (reduced species richness of adult woody plants) harbored a lower species richness and diversity of seedlings. Farmers actively manage the composition of woody plants in their farms. Late

Fig. 5. Seedling species richness per 2 × 2 m subplot within sites in relation to the type of shade tree above, including Albizzia spp. (n = 41), C. africana (n = 22), C. macrostachyus (n = 43), Ficus spp. (n = 11), none (n = 43). Different letters above the boxplots (a and b) indicate statistical differences between the groups. Full species names can be found in Appendix Table S2.
successional species are often eliminated, resulting in a canopy consisting of the common shade tree species and pioneers (e.g. Schmitt et al., 2016; Valencia et al., 2016). These local reductions in woody plant diversity at the site level limits seed availability, making the regeneration of late successional species primarily dependent on dispersal from the surrounding landscape. As expected, we found high species richness and diversity of woody plants as seedlings in sites adjacent to continuous forests, where seed sources are likely not a limiting factor. This shows that trees and shrubs are capable of regenerating in coffee agroforestry systems given that nearby seed sources are present at sufficient densities. Similar patterns have been found in other systems (e.g. tree plantations Senbeta and Teketay, 2001). Dispersal limitation has been suggested to be an important constraint for biodiversity conservation in fragmented landscapes (Mendonça-Lima de et al., 2014; Telilla et al., 2015) and in concordance with this, we found that seedling species richness and diversity declined drastically within a few kilometers from continuous forests. Complementary to seed source abundance, continuous forests are a preferred habitat for many animals and, since the main dispersal mode in the tropics is by frugivores, animal diversity is a further prerequisite for successful dispersal of a diversity of seeds. Sites nearby or adjacent to continuous forests harbor a larger number of animals compared to isolated forest fragments (Cordeiro and Howe, 2001; Bovo et al., 2018; Rodrigues et al., 2018) and animal diversity decreases with distance to forest (e.g. tea agroforestry in India Yashmita-Ulman et al., 2020). In our study area, baboons rarely occur more than 2 km from the forest edge (Lemessa et al., 2013; Samnegård et al., 2014), whereas colobus monkeys are present throughout the landscape (personal observation). Bird diversity was generally shown to be high in agroforestry systems throughout the landscape (Buechley et al., 2015). However, forest specialists were largely reduced with distance to natural forests, likely with implications for their associated seed dispersal (Engelen et al., 2017; Rodrigues et al., 2018). Finally, our results show that distance to continuous forest indirectly affects seedling species richness, diversity and density, mediated by species richness of woody plants and canopy cover in coffee agroforestry. In other words, sites closer to continuous forests generally have a dense and diverse canopy and thereby positively affect woody plant regeneration, presumably by more optimal microclimatic conditions and increased local seed sources, as we discussed earlier.

Not all species were negatively affected by distance to the forest. A number of species regenerated abundantly throughout the landscape. This is reflected in our result that seedling density was not directly associated to distance from continuous forest. Species that were abundant throughout the landscape consisted primarily of common shade trees and pioneers, which are generally not seed limited. Our study included highly managed sites where the adult woody plant community composition was dominated by a few common species (e.g. Albizia spp., C. macrostachyus, Cordia africana and Vernonia auriculifera), which was directly reflected in the seedling community. Additionally, pioneer species are less sensitive to, or even thrive with, human disturbance and have a higher chance to germinate and grow compared to late successional species. In contrast, many late successional species were only found in few of our sites as seedlings (Appendix table, S1) and regenerated primarily nearby continuous forests where seed sources were abundant. Previous studies have also suggested that late successional species were not regenerating in agroforestry systems due to seed limitation (Hundera et al., 2015).

We found that seedling species richness, diversity and density increased with larger areas with tree cover surrounding an agroforestry site, likely by similar mechanisms as discussed above. A larger area with tree cover might simply consist of more seed sources, as it increases the chance of a mature tree species being present (Rosenzweig, 1995; Kumsa et al., 2016). Furthermore, forest specialist animals have been shown to be more abundant in areas with higher forest cover (Banul et al., 2018). Finally, surrounding area with tree cover can have effects on local microclimatic conditions, thereby influencing habitat quality. Smaller forest-fragments will suffer more edge effects such as increased light penetration and temperatures, stronger wind, and lower humidity (Pohlman et al., 2007; Laurance et al., 2011; Magnago et al., 2015), with negative effects on especially late successional vegetation (Laurance et al., 2011; Shumi et al., 2019).

4.3. Conclusion and relevance for conservation

Recently, it has been shown that coffee agroforestry sites in the focal landscape are rapidly losing woody plant diversity due to intensification of management (Geeraert et al., 2019). We show here that natural regeneration of woody plants still occurs in coffee agroforestry systems, but only when the canopy structure is dense and diverse and/or when sites are located nearby continuous forests. We therefore stress that continuous management intensification and deforestation will arrest the potential for many woody plant species to regenerate in coffee agroforestry, by altering the local microclimate, reducing local seed sources and disrupting seed dispersal from the surrounding landscape. Our data suggests a positive feedback loop, as a decline in woody plant regeneration results directly in a further decline of seed sources throughout the landscape, thus decreasing the potential for regeneration and resulting in a simplification of woody plant diversity in coffee systems. A loss of tree biodiversity will likely be directly reflected in loss of its associated flora and fauna, such as epiphytic plants, primates, birds and arthropods (Bisseleua et al., 2009; Norris et al., 2010). Besides the need for conservation of Afrormontane forest biodiversity for its intrinsic value, preservation of forest biodiversity can enhance ecosystem services. These include general forest ecosystem services such as carbon storage, climate regulation, water- and nutrient recycling and erosion control (Franklin and Pindock, 2017), as well as services directly related to coffee sustainability, including pollination, pest control and resilience to climate variation (Tscharntke et al., 2005; Bos et al., 2007a; Mortimer et al., 2018).

The practice of growing coffee under trees maintains canopy cover in the landscape and reduces the conversion of forests to annual crop agriculture (Hylander et al., 2013), which indicates that agroforestry can play an important role in optimizing biodiversity conservation in the landscape. It is the smallholder farmers who make decisions to intensify the production of coffee or to adopt management practices that also maintain biodiversity values. Therefore, coffee agroforestry need not only to become sustainable from an ecological point of view, but also economically for the smallholder farmers. Certification schemes can give an incentive for biodiversity conservation in agricultural systems to improve the revenue even if sometimes the absolute yield is lower (Tscharntke et al., 2005; Hardt et al., 2015). However, certification schemes generally do not consider landscape properties (Stellmacher and Grote, 2011; Tscharntke et al., 2015) and, as indicated in our study and in previous studies (e.g. Tscharntke et al., 2015), a landscape perspective needs to be integrated in certification schemes to optimize biodiversity conservation. For instance, agroforestry systems located far away from continuous forest might be more suitable for conserving common trees and thereby buffering deforestation, enhancing landscape connectivity and providing a habitat for faunal diversity, whereas certification in agroforestry nearby continuous forests (where many species naturally disperse) should focus on the conservation of late successional trees and typical forest biodiversity. Restoration of the diversity of late-successional trees throughout the landscape is another alternative to reduce dispersal limitations and to facilitate natural regeneration of woody plants in the landscape. This could be achieved by introducing a threshold number of late successional species in or adjacent to coffee agroforestry farms as a requirement for certification.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence
the work reported in this paper.

Acknowledgements

We thank Raya A/Oli for assistance in the field and the National Herbarium at Addis Ababa University for providing facilities during species identification. This work was supported by the Swedish Research Council (Grant no. VR2015-0360 to KH).

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi: https://doi.org/10.1016/j.agee.2021.107384.

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