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Highlights

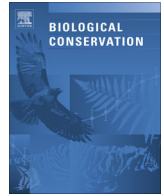
- We compared native woody biodiversity in wild forest fragments and two types of coffee agroforests in southwest Ethiopia.
 - Over 60% of native forest fragment species occurred in semi-forest coffee systems.
 - Intensified coffee plantations contained a much smaller (26%) proportion of native species.
 - Woody species regeneration on semi-forest coffee exceeds that of intensive plantations.
 - Biodiversity persistence in coffee systems relies on source populations in adjacent forest fragments.
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Coffee landscapes as refugia for native woody biodiversity as forest loss continues in southwest Ethiopia

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ABSTRACT

Land-use changes threaten biodiversity and ecosystem services. Some of the last remaining forest fragments in Ethiopia, and the world's only habitats that retain genetically diverse wild Arabica coffee populations, have experienced rapid recent conversion to coffee farms, plantations and agricultural fields. We examined patterns of remnant woody plant diversity in the remaining forests, and assessed the potential and limitations of coffee agroforests to maintain this diversity. We explored patterns of woody biodiversity, structure, and regeneration in forest fragments and on adjacent smallholder and large-scale state-owned shade-coffee farms. A total of 155 native woody species including rare/threatened species of Baphia, Cordia, Manilkara, and Prunus were recorded. Of these species, 56 (36.2%) and 18 (12%) were restricted to forest fragments and coffee farms respectively. Smallholder and large-scale coffee farms maintained 59% and 26% of the 155 recorded native woody species compared to the 137 species (88%) found in forest fragments. Native woody species regeneration in state-owned plantations was lower than in smallholder farms, which in turn was lower than forest fragments. Coffee farms could support a considerable portion, though not all, of the woody biodiversity of disappearing forests. Persistence of forest woody diversity and associated ecosystem services depends strongly on the scale and type of shade coffee cultivation pursued.

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1. Introduction

As tropical deforestation and fragmentation continue, production landscapes will necessarily play important roles in biodiversity conservation (Bhagwat et al., 2008; Gardner et al., 2009). More than 90% of tropical biodiversity is found in human-modified landscapes, outside protected areas (Chazdon et al., 2009). In particular, agricultural landscapes such as shade coffee agroforestry systems (Moguel and Toledo, 1999; Mendez et al., 2007; Gole et al., 2008; Aerts et al., 2011; Hundera et al., 2013a), and home gardens and plantations (Hylander and Nemomissa, 2008, 2009) can serve as biodiversity refugia. However, the amount and composition of biodiversity retained in agroecosystems depends strongly on type of agriculture, and management practices (Harvey et al., 2008). A review by Bhagwat et al. (2008) compared agroforestry systems with nearby forests and showed that the conservation potential of different agroforests varied widely with the taxa in question. Scales and Marsden (2008) described that potentials for biodiversity conservation in agroforests depends on the type of agroforest that is strongly linked to management intensity, economic needs, the extent of remnant forest within the landscape,

cultural practices. Conservation must thus consider carefully the extent and limitations of biodiversity maintenance in production landscapes with particular land-use trajectories.

Traditional coffee agroforests have potential to do better than tea, coffee and oil-palm plantations since such agroforests incorporate shade trees in order to retain ecosystem services such as soil fertility, wood and non-wood products. Coffee agroforestry systems can potentially (1) protect biodiversity by providing heterogeneous and critical habitats, (2) buffer against overexploitation of forest biodiversity, and (3) serve as corridors and permeable matrices that connect meta-communities in natural landscapes (Perfecto et al., 1996). Coffee landscapes may have greater conservation potential in hyper-fragmented landscapes with long histories of human use and disturbance since much of the original forest vegetation is lost and modified.

Only 10% remains of the original vegetation in the Eastern Afromontane biodiversity hotspot with 75% endemism in vascular plants, 40% of it found in Ethiopia (White, 1981; Burgess et al., 2005; Birdlife International, 2012). Within Ethiopia, the large majority of moist Afromontane vegetation and biodiversity occurs in remnant forests in the southwest of the country. Although biophysical and anthropogenic conditions vary, humid Afromontane forests in Ethiopia maintain diverse emergent angiosperms in the overstory; shrubs, herbs, and ferns in the understory; and lianas,

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epiphytes, and lycopods (Friis, 1992). Beyond their high diversity and floristic endemism, these fragments are the only global natural habitats for genetically diverse wild populations of *Arabica* coffee (Gole, 2003; Aerts et al., 2013). Finally, most local people depend on these forests for ecosystem services and goods such as coffee, spices, forest honey, fiber, and fodder (Teketay, 1999; Senbeta and Denich, 2006; Schmitt et al., 2010a). With only a small and declining fraction of remnant forests left, we urgently need to understand the potential for and limitations of coffee agroforestry systems to maintain native woody diversity and associated ecosystem services. The forest fragments we studied are predominantly Afromontane rainforest vegetation and relatively protected, but little managed forests that may or may not have coffee in the understory.

Arabica coffee is the second most traded global commodity after petroleum and the backbone of the Ethiopian economy. Besides being the birthplace of coffee, Ethiopia is the fifth largest global producer of *Arabica* coffee (Tepi Coffee Plantation Enterprise, or TCPE, 2010). In Ethiopia and the study region, coffee is produced under native tree canopies in wild (5%), semi-wild (10%) and plantation systems (85%) (Petit, 2007). Coffee is harvested in the wild either without management, or with management by planting coffee seedlings under natural forest canopy enriched with additional understory management (Wiersum et al., 2005). Semi-forest coffee management is less intensive than plantation coffee, although managing native forests for coffee production reduces specific functional groups or changes the microclimate (Senbeta and Denich, 2006; Aerts et al., 2011; Hundera et al., 2013b). Hundera et al. (2013b) described that intensifying semi-forest coffee to semi-plantation coffee in southwest Ethiopia reduces floristic diversity, stem density, and crown closure. We studied both state-owned (plantations) and smallholder (semi-forest and semi-plantation) coffee systems (Wiersum et al., 2005) adjacent to natural forest-fragments to examine the relative roles of each type of coffee farm in maintaining native woody species diversity, floristic structure and regeneration status.

Smallholder coffee production systems (c. 700,000 ha and 90% of total production in the region), practiced by over 15 million smallholder farmers throughout the nation, are more prevalent than large-scale, state-run coffee production (c. 21,000 ha, 5% of total production) (Petit, 2007). The smallholder farms in the study region range from 0.5 to 3 ha and are composed of wild forests, semi-cultivated forests, plantation and homegardens that vary in management intensity (Weirsum et al., 2005; Tadesse, 2013). The smallholder coffee system in this study comprise semi-forest coffee (67% of our samples), and smallholder managed sand semi-managed and plantations (33%). Only fewer than 10% of small farms are more intensified (less than 10% shade cover, with more coffee density per hectare) and are usually found around homesteads (Tadesse, pers. obs.). Those adjacent to forest fragments were less intensified.

Management in Ethiopia's smallholder coffee farms involves both cultivated and semi-cultivated production, as well as wild coffee, with shade tree selection based on both annual thinning of the original understory vegetation and frequent planting of woody species desirable for shade and other purposes (Senbeta and Denich, 2006; Aerts et al., 2011). In addition to clearing the understory vegetation, farmers frequently tend, transplant, coppice, harvest and replace shade trees for various purposes including beehive construction, fuel wood, furniture and timber.

The state-owned coffee plantations were established mainly between 1975 and 1988 from various landlord-managed and private coffee farms, nationalized after the 1974 revolution, and some recently converted adjacent forests (TCPE, 2010). The three state coffee farms in this study represent the second-largest government plantation area in Ethiopia (2482 hectares) and also cultivate fruits,

spices, and some honey (TCPE, 2010). Although the majority of shade tree species on government farms remained protected at least since early 1980s except if lost by fire or wind fall (TCPE, 2010), people have been replacing native tree species with many native and introduced legumes and shade tree species. Management in these farms is more intensive than the smallholder farms, includes use of machinery (tractors), manual labor for weeding, some use of herbicides and fertilizers, clearing of understory shrubs, and harvesting of coffee that are modified coffee varieties and other tree fruits. Besides native shade tree species, >10 exotic coffee-shade tree species are being introduced in mainly in the state-owned plantations (Tadesse, 2013).

Previous studies on biodiversity conservation in coffee agroforests in southwest Ethiopia focused on woody species diversity (Senbeta and Denich, 2006; Schmitt et al., 2009), mosses and ferns (Hylander and Nemomissa, 2008, 2009), and epiphytic orchids (Hundera et al., 2013a). There are few comparative ecological studies that measure and compare the diversity, structure and regeneration of native woody species among forests and different forms of coffee cultivation (Aerts et al., 2011; Hundera et al., 2012; Hundera et al., 2013a,b). However, there are no known studies that included the more intensified state-owned coffee plantations in the region. We explored the diversity, size structure and regeneration of woody species in remnant forests and the two distinct coffee cultivation systems that continue to expand in southwest Ethiopia. We hypothesize that woody species diversity and regeneration declines as forests are converted into traditional smallholder coffee agroforests and into plantations. We expected that semi-forest and semi-plantation coffee systems have greater roles in conserving native woody species diversity than more intensively managed state-owned coffee plantations.

2. Methods

2.1. Study area

To explore species distribution and diversity patterns among coffee farms and forest-fragments, we studied (1) 18 natural forest patches (2) three state-owned coffee plantations and (3) 39 smallholder coffee farms in 2010 and 2011. We sampled all the three land-cover types that were adjacent to each other with comparable biophysical and climate conditions. The study region included two districts of southwest Ethiopia (1) Yeki (618 km² area) in the Sheka zone (7.2°N, 35.3°E) and (2) Bonga region (2764 km² area) in the Kaffa Zone (36.1°E, 7.1°N) (Fig. 1). Rainfall in the region is uni-modal with annual precipitation of >1600 mm and a mean monthly temperature that ranges from 18 °C to 23 °C (National Meteorological Services Agency, 2008). The two study regions were selected based on the presence of a mosaic of coffee agroforests and forest.

2.2. Data collection

To quantify woody biodiversity, we sampled 115,400-m² plots from 18 forest-fragments of varying size (with a total of 29,794 ha) using transects that run from forest edge to core at 250 m intervals. For larger fragments of >10 ha, we sampled on transects along forest edges (at 300 m from forest fringes) and in forest cores. We also sampled 39,400-m² plots, each owned by different smallholder farms distributed across different elevations and adjacencies to forest fragments and state-owned plantations. A total of 40,400-m² plots were established in the 3 large state-owned plantations (2200 ha), with more plots in larger farms, using systematic random sampling to capture variation in elevation, and management histories (from old to newly established farms).

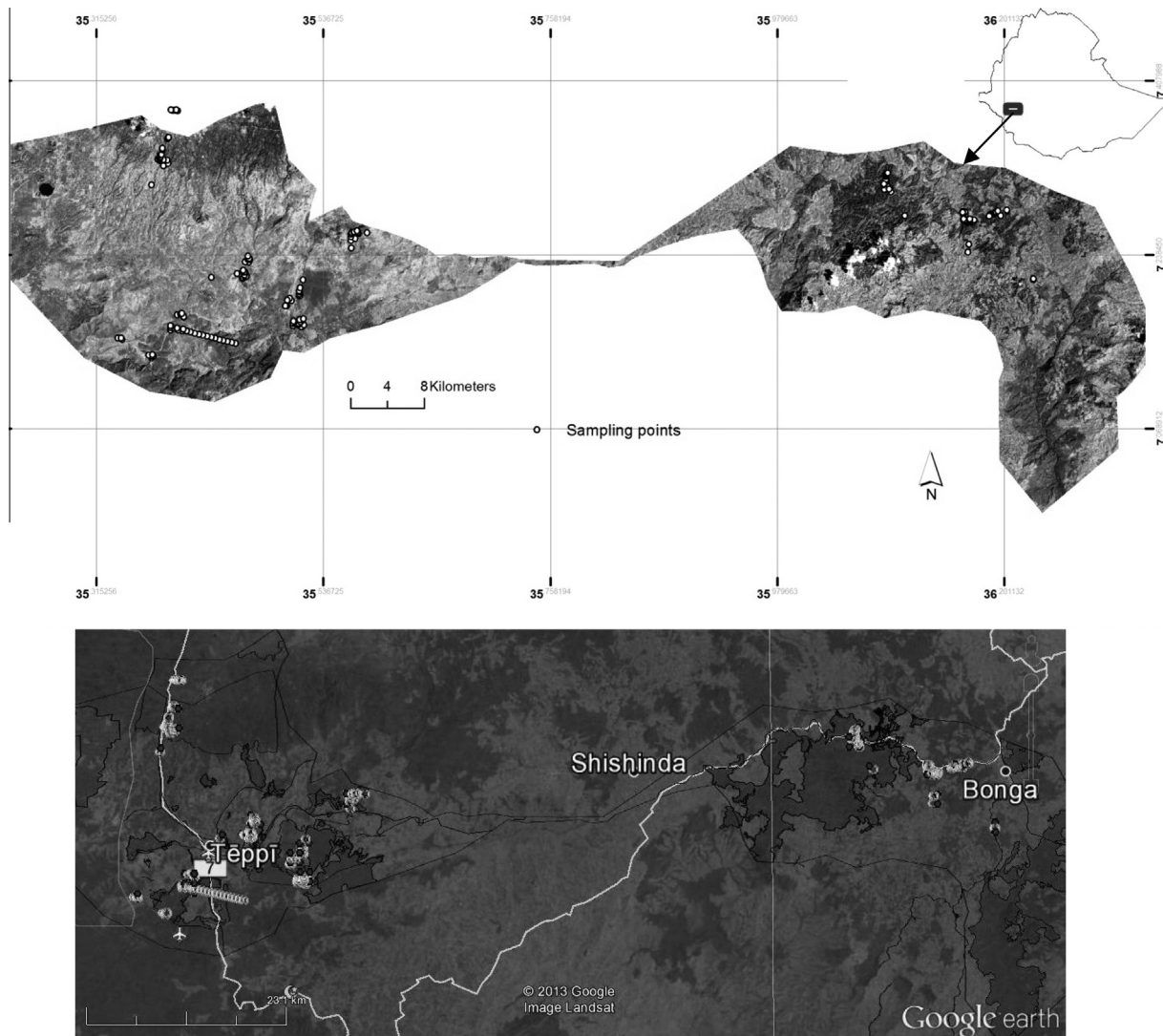


Fig. 1. Map of the study sites in Yeki (left) and Decha (right) districts in southwestern Ethiopia with darker regions indicating forest fragments, and grey representing all other land-use types; circles represent sampling points.

214 In each 400 m²-plot in all the three land-use types, we mea-
 215 sured woody species composition and abundance; canopy closure
 216 or percentage of stand covered by the crowns of live-trees; height;
 217 and DBH for all trees and shrubs >10 cm diameter. We classified
 218 each woody species into four functional groups (trees, small trees
 219 with height <15 m, shrubs and lianas). We used one randomly-located
 220 25 m²-plot nested within each larger plot to census seedlings
 221 (<2 cm DBH) and saplings (2–10 cm DBH) of woody species. DBH
 222 for larger individuals (>10 cm) and height were measured using a
 223 diameter tape and LTI Laser, respectively. We measured altitude
 224 and geographic coordinates for each plot using a Garmin e-Trex
 225 H Portable Navigator, slope using a Suunto clinometer, and canopy
 226 closure using a convex densiometer. We systematically sampled
 227 the three land-use types from lower (1200–1500 m), mid (1500–
 228 2000 m) and higher elevations (2000–2300 m) where we consid-
 229 ered each coffee farms and plantations adjacent to forest fragments
 230 along these gradients.

231 **2.3. Data analyses**

232 Since sample size varied among the two types of coffee systems
 233 and forest fragments, we used individual-based rarefaction using

EstimateS 8.2.0 (Colwell et al., 2012) and R-vegan (Oksanen,
 2011) to estimate species richness in each fragment. We measured
 Shannon diversity (H') and relative abundance (evenness J') of species
 using the Shannon index, compared floristic similarity among
 samples using Jaccard's index (J).

We used one-way ANOVA and Tukey's *post hoc* tests to compare
 species richness, evenness, functional group composition, DBH,
 height, canopy closure and stem density (individuals ha⁻¹) across
 land-cover types. *T*-tests and chi-squares were used to examine
 differences in DBH (cm), height (m), basal area (m² ha⁻¹), and
 canopy closure (m² ha⁻¹) between the edge and core samples in
 larger fragments ($n = 15$). Pearson's coefficient was used to
 correlate species richness with stem density and canopy closure
 in coffee farms.

3. Results

3.1. Overall species diversity

Across all 195,400-m² plots in all three land-use types, we recorded
 155 native woody species belonging to 74 families, dominated by
 Moraceae (9.5%), Rubiaceae (8.7%), Euphorbiaceae (8.2%)

253 and Fabaceae (5.2%). Most of these species were trees (59.4%) and
 254 shrubs (32.9%) with few liana species (8.4%) (Fig. 2). Evergreen species
 255 comprised 66%, with the remaining 34% deciduous. Of the 155
 256 species, 88% (137 spp.) occurred in forest-fragments of which
 257 large-scale and smallholder coffee farms contained 26% (40 spp.)
 258 and 56 % (91 spp.), respectively. An additional 18 native woody
 259 species, 12% of total native flora, were found in the shade coffee
 260 farms but not in the forest-fragments. Species diversity within
 261 woody plant functional groups also differed among the three
 262 land-use types ($F_{2,266} = 15.9, p < 0.001$). Smallholder farms had
 263 fewer species of trees, small trees, shrubs and lianas than natural
 264 forests ($\chi^2_8 = 36.9, p < 0.001$), but more of each type than state-
 265 owned plantations ($p = 0.017$) (Fig. 2).

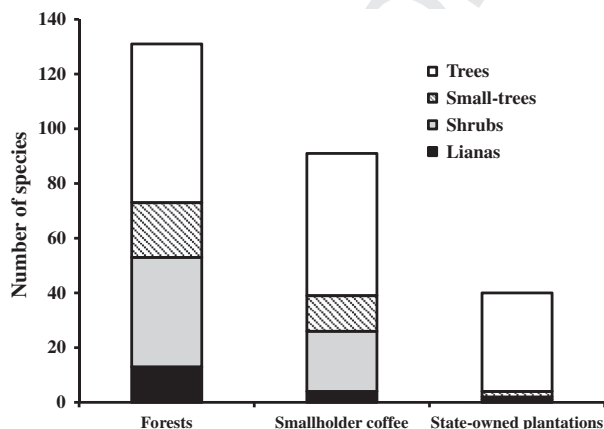
266 3.2. Diversity and structure in the coffee landscapes

267 Individual-based rarefied richness (Table 1) differed significantly
 268 among land-use types ($F_{2,190} = 212.4, p < 0.001$) (Fig. 3).
 269 Mean woody species density per 400 m² in smallholder and state
 270 coffee farms was 7 and 4 respectively, while it was 14 species in
 271 forest-fragments. State-owned farms had significantly lower woody
 272 species richness than forests ($HSD_t = -9.6, p < 0.001$) or smallholder
 273 farms ($HSD_t = -3.2, p = 0.02$). Diversity (H') in natural forests was
 274 greater than in smallholder and state-owned plantations ($F_{2,190}$
 275 $= 220.9, p < 0.001$).

276 Similarly, evenness (J') declined from natural forests to state-
 277 owned plantations (Table 2). No single species made up more than
 278 4% of the total composition in the fragments, while mean dominance
 279 by a single species was 20% and 9% dominant in smallholder
 280 and state-owned plantations, respectively. The five most dominant
 281 species in state-owned and smallholder accounted for 49.5% and
 282 31% of the total individuals respectively, compared to 18.9%
 283 in the forest-fragments.

284 The three land-use types shared 30 species in common, while
 285 56 species were found exclusively in forests, and 4 and 11 species
 286 in large-scale and smallholder respectively. The remaining 64 species
 287 occurred in at least two of the three land-use types. The two
 288 types of coffee farms shared 83% of all tree species and 50% of
 289 the most abundant species in common. Almost all lianas, under-
 290 story shrubs, and many other woody species were restricted to
 291 natural forests.

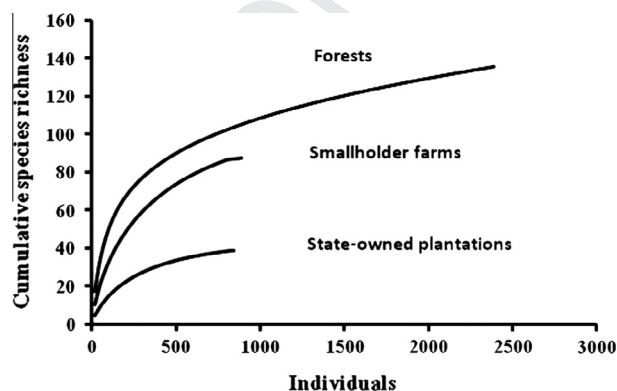
292 Woody species differed in height ($\chi^2 = 52.6, df = 12, p < 0.001$)
 293 and DBH distribution ($\chi^2 = 80.7, df = 8, p < 0.001$) across land-use
 294 types (Table 1). The proportions of juveniles (0–10 cm) and



295 Fig. 2. Plant distribution by growth habit across the three land-use types studied.
 296 Values on the bars indicate the percentage of each habit type relative to the total
 297 number of species found in each land-use, with small trees referring to species that
 298 reach a maximum height of 15 m.

299 **Table 1**
 300 Diversity indices of the three land-use types; DBH and height distribution of woody
 301 plant species by growth form (S = richness), H' (Shannon diversity), and J' (Shannon
 302 evenness), with different superscript letters denoting significantly different values.

	Forests	Smallholder	State-owned
Observed S	137	91	40
Individual-base S	103.2 ^a	86.3 ^b	38.8 ^c
H'	4.1 ^a	3.5 ^b	2.8 ^c
J'	0.85 ^a	0.87 ^b	0.84 ^a
Mean DBH (cm)	36.3 ^a	42.9 ^b	70.2 ^c
Mean height (m)	21.6 ^a	19.5 ^a	29.5 ^b
Basal area (m ² ha ⁻¹)	54.6 ^a	54.5 ^a	57.1 ^b
Mean % canopy	84 ^a	74 ^a	63 ^b
Mature density (ha ⁻¹)	265 ^a	207 ^b	109 ^c
Juvenile density (ha ⁻¹)	258 ^a	113 ^a	58 ^b



303 Fig. 3. Individual-based rarefaction curves for the three land-use types.

304 **Table 2**
 305 Endemic and IUCN red-listed plant species found in the study region (IUCN, <http://www.iucnredlist.org/>; Vivero et al., 2005). LC = Least concern; NT = Near threatened;
 306 VU = Vulnerable, EN = Endangered, NE = Near Endemic; species with * marks indicate
 307 their presence in coffee farms.

Species	Endemic	Threat category
<i>Alstonia boonei</i>		LC
<i>Baphia abyssinica</i>	NE	VU
<i>Bothriocline schimperii</i>	Yes	LC
<i>Erythrina brucei</i> *	Yes	LC
<i>Euphorbia dumalis</i>	Yes	LC
<i>Lipkea adoensis</i> *	Yes	LC
<i>Milicia excelsa</i> *		NT
<i>Millettia ferruginea</i>	Yes	LC
<i>Ocotea kenyensis</i>		VU
<i>Pittosporum abyssinicum</i> *	Yes	
<i>Pouteria altissima</i> *		LC
<i>Prunus africana</i> *		VU
<i>Rinorea friisii</i>	Yes	EN
<i>Solanecio gigas</i> *	Yes	
<i>Tiliacora troupinii</i>	Yes	
<i>Vepris dainellii</i> *	Yes	LC

308 mid-adult (20–50 cm) trees were higher in forests than in small-
 309 holder and State-owned plantations (Fig. 4). However, state-owned
 310 plantations maintained a higher proportion of large adults
 311 (DBH > 1 m) than forest-fragments ($\chi^2 = 28.1, df = 8, p < 0.001$) or
 312 smallholder farms ($\chi^2 = 6.6, df = 4, p = 0.04$) (Fig. 4). Woody species
 313 in smallholder farms had higher seedling (DBH ≤ 5 cm) abundance
 314 than did state-owned plantations ($\chi^2 = 90.8, df = 16, p < 0.001$).

315 Per-hectare density of mature woody individuals in smallholder
 316 farms (207) was greater than on state-owned plantations (109),
 317 but lower than in forest-fragments (265) ($F_{2,192} = 66.5, p < 0.001$).
 318 Smallholder farms had significantly higher stem density
 319 ($HSD_t = 177.4, df = 77, p < 0.001$) than state-owned plantations.

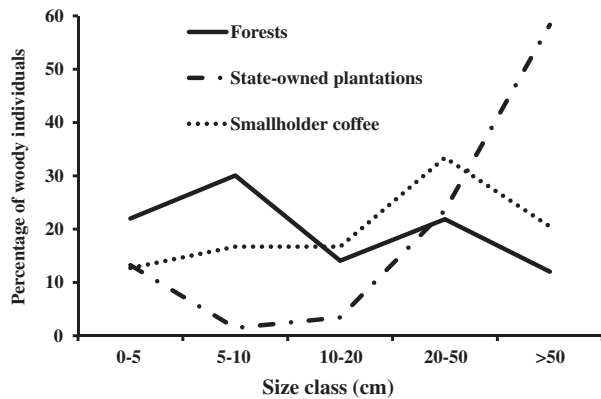


Fig. 4. Size class distribution across the three land-use types.

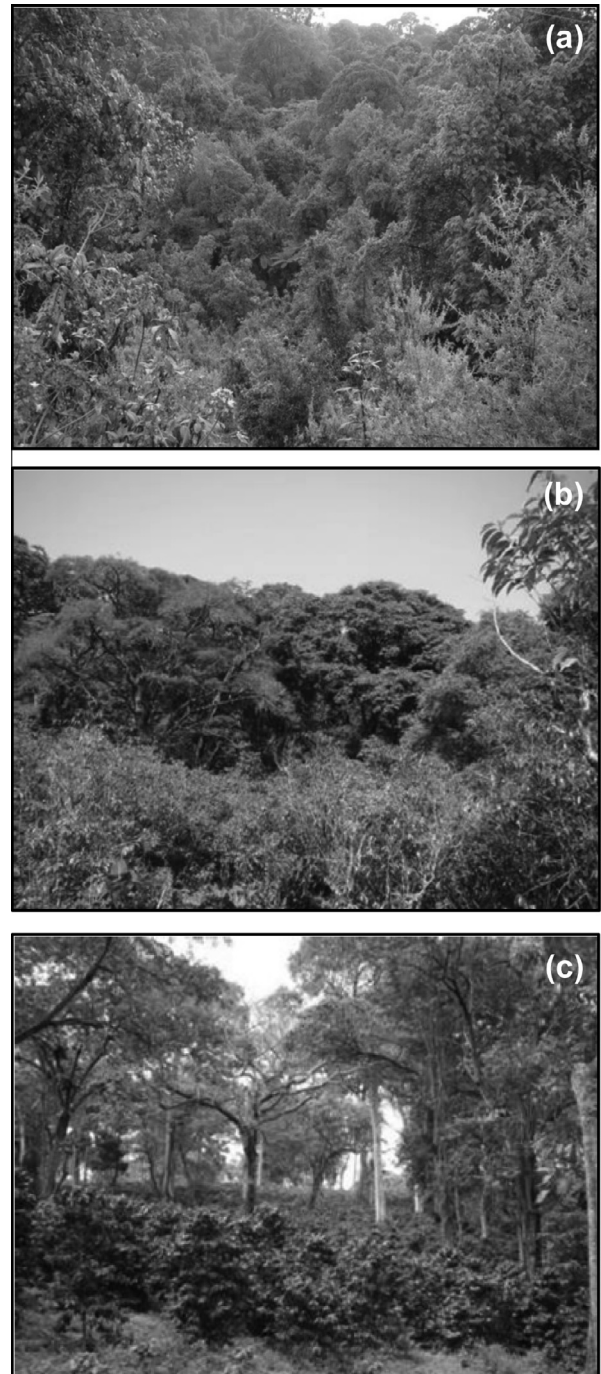


Fig. 5. Vegetation structure of the three land-use types (a) forest fragment with woody species of lower size classes, (b) smallholder semi-forest coffee plantations dominated by mid-size classes of shade trees, and (c) state-owned plantations dominated by large-size shade trees.

Smallholder farms also had higher canopy closure (mean = 72%) than state-owned plantations (mean = 63%) (HSD_t = 8.7, df = 77, p = 0.005) but had similar canopy closure to forest fragments (forest mean = 84%) (p < 0.08). Finally, species richness at the plot scale was significantly correlated with both stem density (Pearson correlation coefficient = 0.87, p < 0.001) and canopy closure (Pearson's correlation coefficient = 0.21, p = 0.054) across the two coffee systems.

Natural forests had higher seedling ($\chi^2 = 18$, df = 12, p = 0.01) and sapling abundance (DBH = 5–10 cm) ($\chi^2 = 495.9$, df = 152, p < 0.001) than smallholder farms, indicating that forest fragments have higher regeneration and recruitment than the semi-forest and semi-plantation coffee of the smallholder farmers. Juvenile density among the three land-use types varied (F_{2,192} = 66.5, p < 0.001) with higher regeneration in smallholder coffee farms than in state-owned plantations (HSD_t = 177.4, p < 0.001). The richness of regenerating species declined by 50% when forests are converted into smallholder semi-forest coffee systems, and by 79% when forests are converted into large-scale plantations. Small-tree, shrub and liana accounted for much of these differences. More than 95% of woody species found in forest fragments are regenerating compared to the 73% species occurred in the smallholder (semi-forest and semi-plantation coffee) and 68% on state-owned coffee (plantations). Regeneration of woody species decreased by 56% when forests are converted into semi-forest and semi-plantation coffee, and by 76% if these forests are converted into large-scale coffee plantations. The skewed size class distribution for state-owned plantations (Fig. 4) also indicates that some of the regenerations are transitory on these plantations, with very little recruitment and that most of the trees are in the largest size classes (Fig. 5).

4. Discussion

We found that in addition to the loss of many old growth populations of tree species and megafauna reported previously (Birdlife International, 2012), our study forests have lower diversity and more threatened taxa than other, better-protected forests in southwest Ethiopia (Gole, 2003). While coffee agroforestry protected significant fractions of forest woody diversity, we found that conversion of forests to traditional coffee agroforests resulted in a loss of at least 34% of forest-based woody species, with an additional 37% loss if intensified to large-scale coffee plantations. Although coffee farms capture only subsets of remnant forest diversity, they maintain important components of woody biodiversity compared to, for example, tea and palm-oil plantations (Hylander et al., 2013). Over 60% of endemic and IUCN-threatened species found in the region also occurred in coffee farms (Vivero

et al., 2008; Table 2). One of the main difference between smallholder farms and state-owned plantations is that smallholder farms use relatively diverse canopies while the plantations use more intensive methods including more introduced and fewer native shade species. Finally, differences between smallholder and state-owned plantations underscore the importance of specific management approaches for maintaining the conservation value of shade-coffee systems (Harvey et al., 2008).

For some groups (12%) of woody species, semi-forest and semi-plantation coffee systems became the last remaining refugia, since most of their original forest habit has already been converted to

agricultural land. In addition to our findings for woody species, found many species of epiphytes and orchids (Hylander and Nemomissa, 2008, 2009; Hylander et al., 2013), and bird species (Gove et al., 2008) are maintained in semi-forest coffee systems. However, other researchers (Schmitt et al., 2010b; Hundera et al., 2013a) found that lianas, herbs, shrubs and orchids were not well conserved in coffee farms.

Our results show that forest fragments provide important biodiversity not maintained on coffee farms and that they are indispensable to maintain the tree diversity of coffee agroforests over longer time scales. Forest fragments have robust woody plant regeneration with relatively even size class distribution. In contrast, regeneration on coffee farms is lower, especially on the more intensified state-owned plantations, raising the question of whether there are important source-sink relationships between forest-fragments and coffee farms, and therefore whether the populations of native woody species in agroforests are self-sustaining without forest-fragments nearby in the landscape. One direct piece of evidence for such source-sink relationships is the observation that forests are actively used by smallholders as sources for seedlings and saplings of woody species to be planted in smallholder coffee farms. Smallholder coffee therefore have somewhat greater conservation potential than a similar area of coffee plantations as currently managed by the state. Coffee management generally has played and continues to play a critical role in determining the spatial distribution of forest cover and the level of forest disturbance in southwestern Ethiopia (Hylander et al., 2013).

Although many of the forest fragments we surveyed are depauperate in relation to less fragmented forests in other Afromontane regions in the region (Friis, 1992; Gole, 2003), our results show that high woody species diversity is still maintained. Ecosystem service dependence could enhance maintenance of diversity; our finding that forest patches containing wild coffee and spices tend to be more diverse is possibly due to protection, provided by users of these services, from widespread logging and disturbance (Hylander et al., 2013; Tadesse, pers. obs.). Here, the presence of coffee plantations may support forest conservation in another way: although wild coffee may have incentivized people to protect fragments from outright destruction over coarse time and spatial scales (McCann, 1997), intensive wild coffee management in forest-fragments would reduce density, regeneration and diversity of tree species (Senbeta and Denich, 2006; Hylander et al., 2013). Coffee plantations will thus reduce pressure on these wild coffee forests.

4.1. Species diversity in coffee landscapes

While elevational gradients, disturbance and fragmentation affected species diversity in natural forests (Tadesse, 2013), tree selection and management of the shade tree canopy strongly influenced diversity in coffee farms. Compared to state-owned plantations, smallholder farms support higher woody species diversity that likely resulted from (1) varying choices of shade-tree species by individual farmers that maintained overall heterogeneity in these landscapes, and (2) lower intensification that allow woody species recruitment unlike in state-owned plantations, where biodiversity decreased with intensification (agrochemical use, conversion of semi-forest into semi-plantation coffee, weed and shade tree management, use of exotic shade tree species, homogenization of farm plots). We found increased species diversity with increased shade tree density in coffee farms (Senbeta and Denich, 2006; Aerts et al., 2011; Hundera et al., 2013b; Hylander et al., 2013) similar to diverse polyculture shade coffee farms in central America (Lopez-Gomez et al., 2007; Mendez et al., 2007).

Forests and smallholder farms, and the two types of coffee farms had more species in common than do forests and state

farms. High similarity in floristic structure and composition between state-owned plantations and smallholder farms occurred due to selection of a similar pool of native species, which are not random assemblages but rather include subsets of forest species that are desirable for optimum shade coffee production. Farmers traditionally prefer tree species that (1) grow high enough to allow optimum light radiation for the understory coffee, (2) provide conducive microclimate, (3) fix nitrogen and provide quality litter as mulch, (4) do not produce fruits which interfere with coffee bean harvesting, and (5) are multipurpose for goods and services including bee forage, beehive hanging sites, timber, fuelwood and construction (see Cerdan et al., 2012; Tadesse, 2013). Our findings show that smallholder semi-forest coffee are species diverse as a result of keeping these species for diverse purposes, due to minimum management and input by coffee growers (Hundera et al., 2013b). Although such production systems have lower productivity with only about 30% of coffee yield per hectare from intensive coffee systems (Wiersum et al., 2005), they can provide landscape diversity and heterogeneity that can further increase matrix quality for the biodiversity in forest fragments (see Perfecto and Vandermeer, 2008; Gardner et al., 2009). The potentials and challenges of biodiversity persistence in these coffee systems provide useful information about the trade-offs and synergies associated with integrating wild biodiversity conservation with agricultural production (Power, 2010; Balmford et al., 2012).

In addition to planned biodiversity for shade coffee, associated biodiversity such as ferns (Yeshitila, 2008), epiphytes (Hylander and Nemomissa, 2008), and birds (Gove et al., 2008) are supported in these farms although likely at lower levels than the forest fragments. Higher woody biodiversity was maintained in individually managed small-farms compared to large state farms or collectively managed cooperatives in Central America (Mendez et al., 2010). Generally, woody species richness in state-owned plantations and smallholder farms in this study is comparable to traditional polyculture and rustic coffee systems of Latin America, respectively (Moguel and Toledo, 1999; Philpott et al., 2008). Tree density in our study coffee systems is also comparable to or higher than the density of some rustic and traditional agroforestry systems in Latin America (Philpott et al., 2008). Canopy closures of the large-scale and smallholder farms in our study were equivalent to respective traditional polyculture and rustic coffee landscapes in Latin America (Moguel and Toledo, 1999) and to semi-forest coffee farms in areas adjacent to our study region (Hundera et al., 2013b).

4.2. Prospects and challenges for conservation in forest-coffee mosaics

Out of forest fragments converted into other land-use types about 25% became traditional coffee farms, and 30% and 15% became cultivated fields, and tea and eucalyptus plantations, respectively (Tadesse, 2013). Given current land-use trends, forest fragments will continue to decline and smallholder coffee farms will have an increasingly significant role as biodiversity repositories and ecosystem service sources. Hylander et al. (2008) described that deforestation risks will be higher in forests without coffee cultivation than in forested landscapes integrated with coffee production. Our results corroborate that smallholder farms particularly, and state-owned plantations to a lesser extent, have great conservation potential besides reducing overexploitation of forest species for fuel wood, charcoal and construction. They will also buffer the effects of disturbance and fragmentation; and act as sources and sinks among meta-communities in these fragmented landscapes, especially for tree species and to a lesser extent for herbs, shrubs, epiphytes and lianas. Hundera et al. (2013a), however, concluded that epiphytic orchids are better conserved in larger and unmanaged forest fragments than in more managed forest-coffee systems implying the need to closely examine the role of

managed forest-coffee systems in conservation of specific taxa and functional groups.

Smallholder farms were almost like forests in structural and life-form diversity, and had more native species and regeneration which implies a relatively high functional diversity that supports more species and ecosystem services. However, the persistence of shade tree populations in these coffee agro-forests rely on the existence of adjacent forest fragments for sources of propagules. The growing management intensity negatively affects the regeneration of woody species; Hundera et al. (2013b) found that regeneration of late-successional tree species is higher in less managed coffee systems compared to that of plantation coffee. The adverse effects of coffee intensification on regeneration of woody species is more evident in the state-owned plantations in this study, where active weeding, use of machinery and herbicides severely affect recruitment although many shade-tree seeds were observed germinating on these plantations. Intensive management on these plantations including the use of herbicides and frequent clearing practices make it unlikely that many seedlings would survive to maturity.

Despite the significant potential of coffee agroforests in biodiversity conservation, homogenization of coffee production standards, cooperativizing small growers, introduced species, population pressure and improved coffee cultivars that thrive under light conditions are ongoing biodiversity challenges in coffee landscapes (Tadesse, 2013). Growing demands for more land and coffee yield could increase transitions from shaded to unshaded, and from wild and semi-wild to garden coffee and plantations. Introduction of exotic shade and non-shade species, and subsequent biotic homogenization has already increased during the last 30 years. For economic reasons, many farmers are preferring fast-growing, introduced *Eucalyptus*, which is replacing native tree species. Extension programs in the region have also been promoting fast-growing exotic agroforestry tree species such as *Grevillea robusta*, *Spathodea campanulata*, *Eucalyptus* spp., and *Sesbania sesban* (Tolera et al., 2008; Tadesse, 2013) as coffee shade, wind breaks, fuelwood and timber. The farmer preference and growth of fast-growing and introduced *Eucalyptus* plantations for economic reasons is replacing native agroforestry tree species (Jenbere et al., 2011). Current trends toward coffee intensification by reducing shade tree density and diversity threaten biodiversity on-farm and in natural forest, as has been reported in several other coffee growing regions (Perfecto et al., 1996; Harvey et al., 2008; Tscharntke et al., 2011; Aerts et al., 2011; Hundera et al., 2013b).

The emerging practices of intensive cereal and spice production following recent market incentives will also threaten the traditional coffee production systems. Promotion of the traditional production systems through coffee certification programs that promote ecological friendly coffee, and other incentives such as payment for environmental services, could help to substantially reduce the rate of woody biodiversity loss in the region (Weirsum et al., 2005; Gole et al., 2008; Aerts et al., 2011).

5. Conclusion

Although the coffee farms may become vital refugia for some species, many other species may not be maintained in these farms if the remaining forest habitats are further disturbed, destroyed, or converted to coffee farms or other agricultural lands. Hence, remaining forest-fragments need to be protected for conserving the species restricted to the forests as well as for the values the remnant fragments provide to local livelihoods. This implies that conservation in coffee agroforests, other working landscapes and forest-fragments needs to be integrated to sustain biodiversity

and ecosystem services for meeting livelihood, cultural and conservation needs.

6. Uncited references

Almeida-Neto et al. (2008), Curtis and McIntosh (1951), Garcia et al. (2010), IUCN (2013), Jenbere et al. (2012), Jose (2012), Lopez-Gomez et al. (2008), Magurran (1988), Oksanen et al. (2010), Rappole et al. (2003), Reusing (2000), Schmitt et al. (2013), Tscharntke et al. (2005), Tesfaye (2006) and Wiersum et al. (2008).

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