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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 stateowned 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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44 **1. Introduction**

45 As tropical deforestation and fragmentation continue, production landscapes will necessarily play important roles in biodiver-46 47 sity conservation (Bhagwat et al., 2008; Gardner et al., 2009). More than 90% of tropical biodiversity is found in human-modified 48 landscapes, outside protected areas (Chazdon et al., 2009). In par-49 ticular, agricultural landscapes such as shade coffee agroforestry 50 51 systems (Moguel and Toledo, 1999; Mendez et al., 2007; Gole 52 04 et al., 2008; Aerts et al., 2011; Hundera et al., 2013a), and home gardens and plantations (Hylander and Nemomissa, 2008, 2009) 53 can serve as biodiversity refugia. However, the amount and com-54 55 position of biodiversity retained in agroecosystems depends strongly on type of agriculture, and management practices (Harvey 56 57 et al., 2008). A review by Bhagwat et al. (2008) compared agroforestry systems with nearby forests and showed that the conserva-58 tion potential of different agroforests varied widely with the taxa 59 in question. Scales and Marsden (2008) described that potentials 60 61 for biodiversity conservation in agroforests depends on the type 62 of agroforest that is strongly linked to management intensity, eco-63 nomic needs, the extent of remnant forest within the landscape,

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0006-3207/\$ - see front matter \odot 2013 Elsevier Ltd. All rights reserved. http://dx.doi.org/10.1016/j.biocon.2013.11.034 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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88 epiphytes, and lycopods (Friis, 1992). Beyond their high diversity 89 and floristic endemism, these fragments are the only global natural 90 habitats for genetically diverse wild populations of Arabica coffee 91 (Gole, 2003; Aerts et al., 2013). Finally, most local people depend 92 on these forests for ecosystem services and goods such as coffee, 93 spices, forest honey, fiber, and fodder (Teketay, 1999; Senbeta 94 and Denich, 2006; Schmitt et al., 2010a). With only a small and 95 declining fraction of remnant forests left, we urgently need to 96 understand the potential for and limitations of coffee agroforestry 97 systems to maintain native woody diversity and associated ecosys-98 tem services. The forest fragments we studied are predominantly 99 Afromontane rainforest vegetation and relatively protected, but lit-100 tle managed forests that may or may not have coffee in the understory. 101

102 Arabica coffee is the second most traded global commodity after 103 petroleum and the backbone of the Ethiopian economy. Besides 104 being the birthplace of coffee. Ethiopia is the fifth largest global 105 producer of Arabica coffee (Tepi Coffee Plantation Enterprise, or 106 TCPE, 2010). In Ethiopia and the study region, coffee is produced under native tree canopies in wild (5%), semi-wild (10%) and plan-107 108 tation systems (85%) (Petit, 2007). Coffee is harvested in the wild 109 either without management, or with management by planting coffee seedlings under natural forest canopy enriched with additional 110 understory management (Wiersum et al., 2005). Semi-forest coffee 111 112 management is less intensive than plantation coffee, although 113 managing native forests for coffee production reduces specific 114 functional groups or changes the microclimate (Senbeta and Denich, 2006; Aerts et al., 2011; Hundera et al., 2013b). Hundera 115 et al. (2013b) described that intensifying semi-forest coffee to 116 117 semi-plantation coffee in southwest Ethiopia reduces floristic 118 diversity, stem density, and crown closure. We studied both state-owned (plantations) and smallholder (semi-forest and 119 120 semi-plantation) coffee systems (Wiersum et al., 2005) adjacent 121 to natural forest-fragments to examine the relative roles of each 122 type of coffee farm in maintaining native woody species diversity, 123 floristic structure and regeneration status.

124 Smallholder coffee production systems (c. 700.000 ha and 90%) 125 of total production in the region), practiced by over 15 million 126 smallholder farmers throughout the nation, are more prevalent 127 than large-scale, state-run coffee production (c. 21,000 ha, 5% of 128 total production) (Petit, 2007). The smallholder farms in the study 129 region range from 0.5 to 3 ha and are composed of wild forests, semi-cultivated forests, plantation and homegardens that vary in 130 131 management intensity (Weirsum et al., 2005; Tadesse, 2013). The smallholder coffee system in this study comprise semi-forest 132 133 coffee (67% of our samples), and smallholder managed sand 134 semi-managed and plantations (33%). Only fewer than 10% of small 135 farms are more intensified (less than 10% shade cover, with more 136 coffee density per hectare) and are usually found around home-137 steads (Tadesse, pers. obs.). Those adjacent to forest fragments 138 were less intensified.

Management in Ethiopia's smallholder coffee farms involves 139 both cultivated and semi-cultivated production, as well as wild 140 coffee, with shade tree selection based on both annual thinning 141 142 of the original understory vegetation and frequent planting of woody species desirable for shade and other purposes (Senbeta and 143 144 Denich, 2006; Aerts et al., 2011). In addition to clearing the understory vegetation, farmers frequently tend, transplant, coppice, 145 harvest and replace shade trees for various purposes including bee-146 147 hive 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 154 shade tree species on government farms remained protected at 155 least since early 1980s except if lost by fire or wind fall (TCPE, 156 2010), people have been replacing native tree species with many 157 native and introduced legumes and shade tree species. Manage-158 ment in these farms is more intensive than the smallholder farms, 159 includes use of machinery (tractors), manual labor for weeding, 160 some use of herbicides and fertilizers, clearing of understory 161 shrubs, and harvesting of coffee that are modified coffee varieties 162 and other tree fruits. Besides native shade tree species, >10 exotic 163 coffee-shade tree species are being introduced in mainly in the 164 state-owned plantations (Tadesse, 2013). 165

Previous studies on biodiversity conservation in coffee agrofor-166 ests in southwest Ethiopia focused on woody species diversity 167 (Senbeta and Denich, 2006; Schmitt et al., 2009), mosses and ferns 168 (Hylander and Nemomissa, 2008, 2009), and epiphytic orchids 169 (Hundera et al., 2013a). There are few comparative ecological stud-170 ies that measure and compare the diversity, structure and regen-171 eration of native woody species among forests and different forms 172 of coffee cultivation (Aerts et al., 2011; Hundera et al., 2012; Hun-173 dera et al., 2013a,b). However, there are no known studies that in- 05 174 cluded the more intensified state-owned coffee plantations in the 175 region. We explored the diversity, size structure and regeneration 176 of woody species in remnant forests and the two distinct coffee 177 cultivation systems that continue to expand in southwest Ethiopia. 178 We hypothesize that woody species diversity and regeneration de-179 clines as forests are converted into traditional smallholder coffee 180 agroforests and into plantations. We expected that semi-forest 181 and semi-plantation coffee systems have greater roles in conserv-182 ing native woody species diversity than more intensively managed 183 state-owned coffee plantations. 184

- 2. Methods
- 2.1. Study area

To explore species distribution and diversity patterns among 187 coffee farms and forest-fragments, we studied (1) 18 natural forest 188 patches (2) three state-owned coffee plantations and (3) 39 small-189 holder coffee farms in 2010 and 2011. We sampled all the three 190 land-cover types that were adjacent to each other with comparable 191 biophysical and climate conditions. The study region included two 192 districts of southwest Ethiopia (1) Yeki (618 km² area) in the Sheka 193 zone (7.2°N, 35.3°E) and (2) Bonga region (2764 km² area) in the 194 Kaffa Zone (36.1°E, 7.1°N) (Fig. 1). Rainfall in the region is uni-mod-195 al with annual precipitation of >1600 mm and a mean monthly 196 temperature that ranges from 18 °C to 23 °C (National Meteorolog-197 ical Services Agency, 2008). The two study regions were selected 198 based on the presence of a mosaic of coffee agroforests and forest. 199

2.2. Data collection

To quantify woody biodiversity, we sampled 115,400-m² plots 201 from 18 forest-fragments of varying size ($\widehat{\mathbf{w}}$ ith a total of 202 29,794 ha) using transects that run from forest edge to core at 203 250 m intervals. For larger fragments of >10 ha, we sampled on 204 transects along forest edges (at 300 m from forest fringes) and in 205 forest cores. We also sampled 39,400-m² plots, each owned by dif-206 ferent smallholder farms distributed across different elevations 207 and adjacencies to forest fragments and state-owned plantations. 208 A total of 40,400-m² plots were established in the 3 large state-209 owned plantations (2200 ha), with more plots in larger farms, 210 using systematic random sampling to capture variation in eleva-211 tion, and management histories (from old to newly established 212 213 farms).



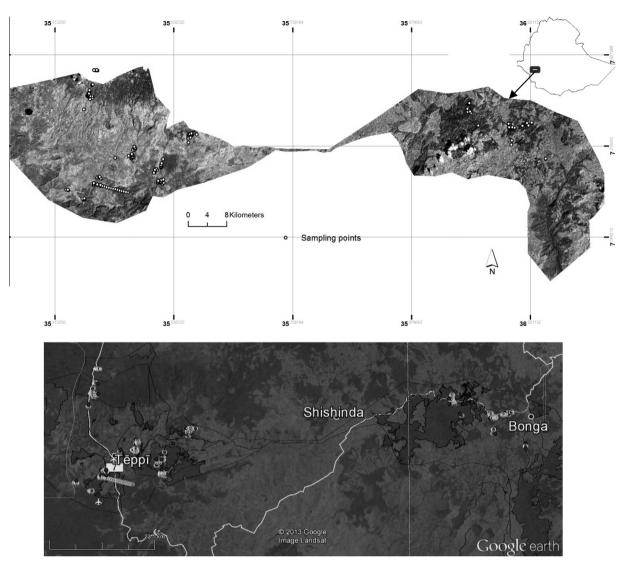


Fig. 1. Map of the study sites in Yeki (left) and Decha (right) districts in southwestern Ethiopia with darker regions indicating forest fragments, and grey representing all other land-use types; circles represent sampling points.

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

EstimateS 8.2.0 (Colwell et al., 2012) and R-vegan (Oksanen, 234 2011) to estimate species richness in each fragment. We measured 235 Shannon diversity (H') and relative abundance (evenness J') of species using the Shannon index, compared floristic similarity among 237 samples using Jaccard's index (J) . 238 We used one-way ANOVA and Tukey's post hoc tests to com-239

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. <u>T-tests</u> 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

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231 2.3. Data analyses

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

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%) 252

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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 spe-255 cies 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 farms but not in the forest-fragments. Species diversity within 260 261 woody plant functional groups also differed among the three land-use types ($F_{2,266}$ = 15.9, p < 0.001). Smallholder farms had 262 fewer species of trees, small trees, shrubs and lianas than natural 263 264 forests (χ_8^2 = 36.9, *p* < 0.001), but more of each type than stateowned plantations (p = 0.017) (Fig. 2). 265

266 3.2. Diversity and structure in the coffee landscapes

267 06 Individual-based rarefied richness (Table 1) differed significantly among land-use types ($F_{2,190} = 212.4$, p < 0.001) (Fig. 3). 268 Mean woody species density per 400 m^2 in smallholder and state 269 270 coffee farms was 7 and 4 respectively, while it was 14 species in 271 forest-fragments. State-owned farms had significantly lower woo-272 dy species richness than forests (HSD_{t = -9.6, p < 0.001) or smallholder} farms (HSD_t = -3.2, p = 0.02). Diversity (H') in natural forests was 273 greater than in smallholder and state-owned plantations $(F_{2,190})$ 274 = 220.9, *p* < 0.001). 275

276 Similarly, evenness (I') 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 domi-279 nance 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% in 283 the forest-fragments.

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

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

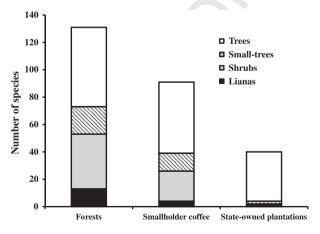


Fig. 2. Plant distribution by growth habit across the three land-use types studied. Values on the bars indicate the percentage of each habit type relative to the total number of species found in each land-use, with small trees referring to species that reach a maximum height of 15 m.

Table 1

Diversity indices of the three land-use types; DBH and height distribution of woody plant species by growth form (S = richness), H' (Shannon diversity), and J' (Shannon 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 (m² 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

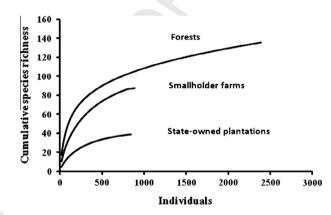


Fig. 3. Individual-based rarefaction curves for the three land-use types.

Table 2

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; VU = Vulnerable, EN = Endangered, NE = Near Endemic; species with * marks indicate their presence in coffee farms.

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

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

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

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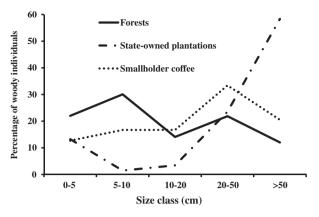


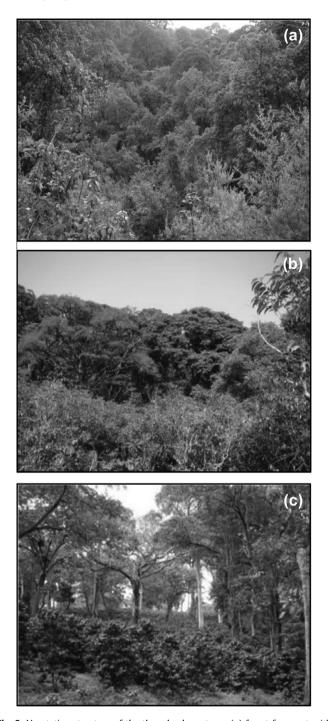
Fig. 4. Size class distribution across the three land-use types.

307 Smallholder farms also had higher canopy closure (mean = 72%) 308 than state-owned plantations (mean = 63%) (HSD_t = 8.7, df = 77, p = 0.005) but had similar canopy closure to forest fragments (for-309 310 est mean = 84%) (p < 0.08). Finally, species richness at the plot scale was significantly correlated with both stem density (Pearson corre-311 lation coefficient = 0.87, p < 0.001) and canopy closure (Pearson's 312 correlation coefficient = 0.21, p = 0.054) across the two coffee 313 systems. 314

Natural forests had higher seedling ($\chi^2 = 18$, df = 12, p = 0.01) 315 and sapling abundance $(DBH = 5-10 \text{ cm})^{-1}(\chi^2 = 495.9, \text{ df} = 152,$ 316 p < 0.001) than smallholder farms, indicating that forest fragments 317 have higher regeneration and recruitment than the semi-forest and 318 319 semi-plantation coffee of the smallholder farmers. Juvenile density among the three land-use types varied $(F_{2,192} = 66.5, p < 0.001)$ 320 with higher regeneration in smallholder coffee farms than in 321 state-owned plantations (HSD_t = 177.4, p < 0.001). The richness of 322 regenerating species declined by 50% when forests are converted 323 324 into smallholder semi-forest coffee systems, and by 79% when for-325 ests are converted into large-scale plantations. Small-tree, shrub 326 and liana accounted for much of these differences. More than 327 95% of woody species found in forest fragments are regenerating 328 compared to the 73% species occurred in the smallholder (semi-329 forest and semi-plantation coffee) and 68% on state-owned coffee (plantations). Regeneration of woody species decreased by 56% 330 when forests are converted into semi-forest and semi-plantation 331 coffee, and by 76% if these forests are converted into large-scale 332 333 coffee plantations. The skewed size class distribution for state-334 owned plantations (Fig. 4) also indicates that some of the regenerations are transitory on these plantations, with very little 335 recruitment and that most of the trees are in the largest size classes 336 (Fig. 5). 337

338 4. Discussion

We found that in addition to the loss of many old growth pop-339 ulations of tree species and megafauna reported previously(Birdlife 340 International, 2012), our study forests have lower diversity and 341 more threatened taxa than other, better-protected forests in south-342 343 west Ethiopia (Gole, 2003). While coffee agroforestry protected significant fractions of forest woody diversity, we found that 344 conversion of forests to traditional coffee agroforests resulted in 345 346 a loss of at least 34% of forest-based woody species, with an additional 37% loss if intensified to large-scale coffee plantations. 347 Although coffee farms capture only subsets of remnant forest 348 diversity, they maintain important components of woody biodiver-349 350 sity compared to, for example, tea and palm-oil plantations 351 (Hylander et al., 2013). Over 60% of endemic and IUCN-threatened 352 species found in the region also occurred in coffee farms (Vivero



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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.

et al., 2008; Table 2). One of the main difference between smallholder farms and state-owned plantations is that small-holder 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 semiplantation coffee systems became the last remaining refugia, since most of their original forest habit has already been converted to

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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.

371 Our results show that forest fragments provide important biodi-372 versity not maintained on coffee farms and that they are indispens-373 able to maintain the tree diversity of coffee agroforests over longer time scales. Forest fragments have robust woody plant regenera-374 375 tion with relatively even size class distribution. In contrast, regen-376 eration on coffee farms is lower, especially on the more intensified state-owned plantations, raising the question of whether there are 377 378 important source-sink relationships between forest-fragments and 379 coffee farms, and therefore whether the populations of native woo-380 dy species in agroforests are self-sustaining without forest-frag-381 ments nearby in the landscape. One direct piece of evidence for 382 such source-sink relationships is the observation that forests are 383 actively used by smallholders as sources for seedlings and saplings 384 of woody species to be planted in smallholder coffee farms. Small-385 holder coffee therefore have somewhat greater conservation po-386 tential than a similar area of coffee plantations as currently 387 managed by the state. Coffee management generally has played 388 and continues to play a critical role in determining the spatial dis-389 tribution of forest cover and the level of forest disturbance in 390 southwestern Ethiopia (Hylander et al., 2013).

391 Although many of the forest fragments we surveyed are depau-392 perate in relation to less fragmented forests in other Afromontane 393 regions in the region (Friis, 1992; Gole, 2003), our results show 394 that high woody species diversity is still maintained. Ecosystem 395 service dependence could enhance maintenance of diversity; our 396 finding that forest patches containing wild coffee and spices tend 397 to be more diverse is possibly due to protection, provided by users 398 of these services, from widespread logging and disturbance 399 (Hylander et al., 2013; Tadesse, pers. obs.). Here, the presence of 400 coffee plantations may support forest conservation in another 401 way: although wild coffee may have incentivized people to protect 402 fragments from outright destruction over coarse time and spatial 403 scales (McCann, 1997), intensive wild coffee management in for-404 est-fragments would reduce density, regeneration and diversity of tree species (Senbeta and Denich, 2006; Hylander et al., 2013). 405 Coffee plantations will thus reduce pressure on these wild coffee 406 407 forests.

408 *4.1. Species diversity in coffee landscapes*

409 While elevational gradients, disturbance and fragmentation af-410 fected species diversity in natural forests (Tadesse, 2013), tree 411 selection and management of the shade tree canopy strongly influ-412 enced diversity in coffee farms. Compared to state-owned plantations, smallholder farms support higher woody species diversity 413 that likely resulted from (1) varying choices of shade-tree species 414 by individual farmers that maintained overall heterogeneity in 415 416 these landscapes, and (2) lower intensification that allow woody 417 species recruitment unlike in state-owned plantations, where biodiversity decreased with intensification (agrochemical use, conver-418 419 sion of semi-forest into semi-plantation coffee, weed and shade 420 tree management, use of exotic shade tree species, homogenization 421 of farm plots). We found increased species diversity with increased 422 shade tree density in coffee farms (Senbeta and Denich, 2006; 423 Aerts et al., 2011; Hundera et al., 2013b; Hylander et al., 2013) sim-424 ilar to diverse polyculture shade coffee farms in central America 425 (Lopez-Gomez et al., 2007; Mendez et al., 2007).

426 Forests and smallholder farms, and the two types of coffee 427 farms had more species in common than do forests and state farms. High similarity in floristic structure and composition be-428 tween state-owned plantations and smallholder farms occurred 429 due to selection of a similar pool of native species, which are 430 not random assemblages but rather include subsets of forest spe-431 cies that are desirable for optimum shade coffee production. Farm-432 ers traditionally prefer tree species that (1) grow high enough to 433 allow optimum light radiation for the understory coffee, (2) pro-434 vide conducive microclimate, (3) fix nitrogen and provide quality 435 litter as mulch, (4) do not produce fruits which interfere with cof-436 fee bean harvesting, and (5) are multipurpose for goods and ser-437 vices including bee forage, beehive hanging sites, timber, 438 fuelwood and construction (see Cerdan et al., 2012; Tadesse, 439 2013). Our findings show that smallholder semi-forest coffee are 440 species diverse as a result of keeping these species for diverse pur-441 poses, due to minimum management and input by coffee growers 442 (Hundera et al., 2013b). Although such production systems have 443 lower productivity with only about 30% of coffee yield per hectare 444 from intensive coffee systems (Wiersum et al., 2005), they can pro-445 vide landscape diversity and heterogeneity that can further in-446 crease matrix quality for the biodiversity in forest fragments (see 447 Perfecto and Vandermeer, 2008; Gardner et al., 2009). The poten-448 tials and challenges of biodiversity persistence in these coffee sys-449 tems provide useful information about the trade-offs and synergies 450 associated with integrating wild biodiversity conservation with 451 agricultural production (Power, 2010; Balmford et al., 2012). 452

In addition to planned biodiversity for shade coffee, associated 453 biodiversity such as ferns (Yeshitila, 2008), epiphytes (Hylander 454 and Nemomissa, 2008), and birds (Gove et al., 2008) are supported 455 in these farms although likely at lower levels than the forest frag-456 ments. Higher woody biodiversity was maintained in individually 457 managed small-farms compared to large state farms or collectively 458 managed cooperatives in Central America (Mendez et al., 2010). 459 Generally, woody species richness in state-owned plantations 460 and smallholder farms in this study is comparable to traditional 461 polyculture and rustic coffee systems of Latin America, respectively 462 (Moguel and Toledo, 1999; Philpott et al., 2008). Tree density in 463 our study coffee systems is also comparable to or higher than the 464 density of some rustic and traditional agroforestry systems in Latin 465 America (Philpott et al., 2008). Canopy closures of the large-scale 466 and smallholder farms in our study were equivalent to respective 467 traditional polyculture and rustic coffee landscapes in Latin Amer-468 ica (Moguel and Toledo, 1999) and to semi-forest coffee farms in 469 areas adjacent to our study region (Hundera et al., 2013b). 470

4.2. Prospects and challenges for conservation in forest-coffee mosaics 471

Out of forest fragments converted into other land-use types 472 about 25% became traditional coffee farms, and 30% and 15% be-473 came cultivated fields, and tea and eucalyptus plantations, respec-474 tively (Tadesse, 2013). Given current land-use trends, forest 475 fragments will continue to decline and smallholder coffee farms 476 will have an increasingly significant role as biodiversity reposito-477 ries and ecosystem service sources. Hylander et al. (2008) de-478 scribed that deforestation risks will be higher in forests without 479 coffee cultivation than in forested landscapes integrated with cof-480 fee production. Our results corroborate that smallholder farms par-481 ticularly, and state-owned plantations to a lesser extent, have great 482 conservation potential besides reducing overexploitation of forest 483 species for fuel wood, charcoal and construction. They will also 484 buffer the effects of disturbance and fragmentation; and act as 485 sources and sinks among meta-communities in these fragmented 486 landscapes, especially for tree species and to a lesser extent for 487 herbs, shrubs, epiphytes and lianas. Hundera et al. (2013a), how-488 ever, concluded that epiphytic orchids are better conserved in 489 larger and unmanaged forest fragments than in more managed for-490 est-coffee systems implying the need to closely examine the role of 491

functional groups.

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6. Uncited references

vation needs.

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 562 al. (2008). 07

and ecosystem services for meeting livelihood, cultural and conser-

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494 Smallholder farms were almost like forests in structural and 495 life-form diversity, and had more native species and regeneration 496 which implies a relatively high functional diversity that supports more species and ecosystem services. However, the persistence 497 498 of shade tree populations in these coffee agro-forests rely on the existence of adjacent forest fragments for sources of propagules. 499 The growing management intensity negatively affects the regener-500 ation of woody species; Hundera et al. (2013b) found that regener-501 ation of late-successional tree species is higher in less managed 502 503 coffee systems compared to that of plantation coffee. The adverse effects of coffee intensification on regeneration of woody species 504 is more evident in the state-owned plantations in this study, where 505 506 active weeding, use of machinery and herbicides severely affect 507 recruitment although many shade-tree seeds were observed germinating on these plantations. Intensive management on these 508 509 plantations including the use of herbicides and frequent clearing practices make it unlikely that many seedlings would survive to 510 511 maturity.

managed forest-coffee systems in conservation of specific taxa and

512 Despite the significant potential of coffee agroforests in biodi-513 versity conservation, homogenization of coffee production standards, cooperativizing small growers, introduced species, 514 population pressure and improved coffee cultivars that thrive un-515 516 der light conditions are ongoing biodiversity challenges in coffee 517 landscapes (Tadesse, 2013). Growing demands for more land and coffee yield could increase transitions from shaded to unshaded, 518 and from wild and semi-wild to garden coffee and plantations. 519 Introduction of exotic shade and non-shade species, and subse-520 521 quent biotic homogenization has already increased during the last 522 30 years. For economic reasons, many farmers are preferring fastgrowing, introduced Eucalyptus, which is replacing native tree spe-523 cies. Extension programs in the region have also been promoting 524 fast-growing exotic agroforestry tree species such as Grevillea ro-525 526 busta, Spathodea campanulata, Eucalyptus spp., and Sesbania sesban 527 (Tolera et al., 2008; Tadesse, 2013) as coffee shade, wind breaks, 528 fuelwood and timber. The farmer preference and growth of fast-529 growing and introduced Eucalyptus plantations for economic reasons is replacing native agroforestry tree species (Jenbere et al., 530 531 2011). Current trends toward coffee intensification by reducing shade tree density and diversity threaten biodiversity on-farm 532 and in natural forest, as has been reported in several other coffee 533 growing regions (Perfecto et al., 1996; Harvey et al., 2008; 534 535 Tscharntke et al., 2011; Aerts et al., 2011; Hundera et al., 2013b).

The emerging practices of intensive cereal and spice production 536 537 following recent market incentives will also threaten the tradi-538 tional coffee production systems. Promotion of the traditional pro-539 duction systems through coffee certification programs that 540 promote ecological friendly coffee, and other incentives such as 541 payment for environmental services, could help to substantially re-542 duce the rate of woody biodiversity loss in the region (Weirsum et al., 2005; Gole et al., 2008; Aerts et al., 2011). 543

5. Conclusion 544

Although the coffee farms may become vital refugia for some 545 species, many other species may not be maintained in these farms 546 547 if the remaining forest habitats are further disturbed, destroyed, or 548 converted to coffee farms or other agricultural lands. Hence, 549 remaining forest-fragments need to be protected for conserving 550 the species restricted to the forests as well as for the values the 551 remnant fragments provide to local livelihoods. This implies that 552 conservation in coffee agroforests, other working landscapes and 553 forest-fragments needs to be integrated to sustain biodiversity

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