



Conservation value of moist evergreen Afromontane forest sites with different management and history in southwestern Ethiopia



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ABSTRACT

Tropical forest ecosystems harbor high biodiversity, but they have suffered from ongoing human-induced degradation. We investigated the conservation value of moist evergreen Afromontane forest sites across gradients of site-level disturbance, landscape context and forest history in southwestern Ethiopia. We surveyed woody plants at 108 randomly selected sites and grouped them into forest specialist, pioneer, and generalist species. First, we investigated if coffee dominance, current distance from the forest edge, forest history, heat load and altitude structured the variation in species composition using constrained correspondence analysis. Second, we modelled species richness in response to the same explanatory variables. Our findings show that woody plant community composition was significantly structured by altitude, forest history, coffee dominance and current distance from forest edge. Specifically, (1) total species richness and forest specialist species richness were affected by coffee management intensity; (2) forest specialist species richness increased, while pioneer species decreased with increasing distance from the forest edge; and (3) forest specialist species richness was lower in secondary forest compared to in primary forest. These findings show that coffee management intensity, landscape context and forest history in combination influence local and landscape level biodiversity. We suggest conservation strategies that foster the maintenance of large undisturbed forest sites and that prioritize local species in managed and regenerating forests. Creation of a biosphere reserve and shade coffee certification could be useful to benefit both effective conservation and people's livelihoods.

1. Introduction

Tropical forest ecosystems host the richest terrestrial biodiversity and provide important local, regional and global human benefits through provisioning, regulating, supporting and cultural ecosystem services (MA, 2005; Lewis et al., 2015). However, tropical primary forests, including strictly protected areas, are suffering from human induced degradation (Wittemyer et al., 2008; Gibson et al., 2011; Melo et al., 2013). While tropical deforestation has long received attention, forest degradation and its consequences are increasingly also considered to be important (Edwards et al., 2014; Edwards, 2016; Barlow et al., 2016).

In a context of gradual forest degradation, forest species diversity and composition (i.e. the various proportions of different species) are

shaped by three major factors, namely (i) site-level disturbance (e.g., see Schmitt et al., 2010), (ii) landscape context, and (iii) forest history (e.g. primary versus secondary forest) (Chazdon, 2008; Barlow et al., 2016). Site-level disturbance includes recurrent and unsustainable logging, hunting, forest fire, fuelwood collection, livestock grazing, and forest management for coffee production (Hundera et al., 2013; Thompson et al., 2013). Such disturbance, in turn, is related to various socio-economic drivers from the level of households to global markets, and can take place legally or illegally (Lambin et al., 2001; Lewis et al., 2015). Forest landscape context influences forest composition via edge effects, which are the abiotic and biotic changes associated with boundaries between forest and non-forest habitats (Harper et al., 2005; Ewers and Didham, 2006; Laurance et al., 2006). Forest history can result in various legacy effects, including immigration credits (Shumi

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et al., 2018) that cause delays in species recovery within secondary forest (Foster et al., 2003; Chazdon, 2008).

Different woody plant species can be expected to respond differently to forest sites with different degrees of site level disturbance, landscape contexts and histories. Slow growing, shade-tolerant specialist species should persist primarily in relatively stable or less disturbed sites, whereas faster growing pioneer and generalist species may favor more disturbed sites (Sheil and Heist, 2000). For instance, Primack and Lee (1991) noticed a change in species composition from shade-tolerant to pioneer species in sites disturbed by logging in Bornean rainforests. Pioneer and generalist species should respond positively to edge effects, while forest specialist species should respond negatively and should be more abundant in sites deep within the forest (Harper et al., 2005). Species recovery in secondary forest should depend on the extent and intensity of past land use, as well as the surrounding vegetation – for example, most tropical secondary forests on post-agricultural land are dominated by fast-growing pioneer species (Foster et al., 2003; Chazdon, 2008). Although these mechanisms are intuitively appealing, relatively few studies have systematically compared largely undisturbed primary sites with disturbed sites, or have separately assessed the effect of site level disturbance, landscape context and forest history.

Here, we investigate woody plant species composition and richness in forest sites spanning gradients in site-level disturbance (especially coffee management, although we are aware of other disturbances such as firewood collection, logging and grazing), landscape context (distance from the edge) and forest history (primary versus secondary forest) in southwestern Ethiopia. The vegetation in the region is moist evergreen Afromontane forest (Friis et al., 2010). It is the center of origin and diversity of *Coffea arabica* L., still harbors the gene pool of wild coffee populations (Anthony et al., 2002), and is part of the Eastern Afromontane Biodiversity Hotspot (Schmitt, 2006). Over the last few decades, deforestation for agricultural land, settlements and timber extraction has been rapid in the area (Reusing, 2000; Tadesse et al., 2014b; Getahun et al., 2017). Moreover, local people use the forest to obtain fuelwood, construction wood, and farm tools, as well as for livestock grazing, medicine, spices, honey and coffee production (Ango, 2016; Dorresteijn et al., 2017).

Traditionally, coffee is grown and managed in Afromontane forests with varying intensity, ranging from relatively undisturbed wild forest coffee fruit collection to intensively managed semi-plantation coffee systems, where undergrowth plants including herbs, shrubs and trees are cleared; canopy trees are selectively thinned out; and additional coffee seedlings are planted to increase coffee yield (Schmitt et al., 2010; Hundera et al., 2013). In some instances, intensification also involves the removal and replacement of native trees with exotic species, use of herbicides, fertilizers and improved coffee varieties (Wiersum et al., 2008; Tadesse et al., 2014a). There are two divergent observations about coffee forest management. On the one hand, via providing an economic incentive, managing the forest for coffee production has historically helped to slow down deforestation rates (Hylander et al., 2013a). However, at the same time, increasingly intensive coffee production has been linked to forest degradation and loss of local biodiversity (Schmitt et al., 2010; Aerts et al., 2011; Hundera et al., 2013).

Considering ongoing and historical site-level and landscape-level changes, as well as the global importance of moist evergreen Afromontane forests, we sought to investigate how woody plant species composition and richness vary along a gradient of (1) coffee management; (2) forest landscape context (from forest edge to deep inside the forest); and (3) forest history (secondary versus primary forest).

2. Methods

2.1. Study area

The study was conducted in five *kebeles* (the smallest administrative unit in Ethiopia) of three districts (woredas): Gera, Gummay and

Setema of Jimma Zone, Oromia Regional State, southwestern Ethiopia (Fig. 1). The study area comprised a mosaic of land use types, with forest cover ranging from 37 to 84% in the five *kebeles*, while arable land, grazing land and settlements accounted for the rest. The region comprises undulating slopes and flat plateaus, with elevation ranging from 1500 to 3000 m above sea level. The area has a warm moist climate, driven by the dynamics of the inter-tropical convergence zone, with 1500–2000 mm of annual rainfall, and a 20 °C mean annual temperature. The area has unimodal rainfall patterns, with some rain throughout most of the year, and more substantial summer rain primarily from June to September (Friis et al., 2010; Schmitt et al., 2013; Ango, 2016).

The dominant tree species in moist evergreen Afromontane forest include *Olea welwitschii*, *Pouteria adolfi-friederici*, *Schefflera abyssinica*, *Prunus africana*, *Albizia* spp., *Syzygium guineense*, and *Cordia africana* (Cheng et al., 1998). *Coffea arabica* is native to the forest and grows naturally at altitudes between 1000 and 2000 m above sea level (Schmitt, 2006; Senbeta et al., 2014). Coffee and to a lesser degree honey are economically important non-timber forest products. Agriculture including crops and livestock is the main source of livelihoods, and can lead to degradation (e.g. via overgrazing) and encroachment of forested areas (Kassa et al., 2016).

2.2. Land cover mapping and study site selection

Our design sought to capture broad gradients in site-level conditions, landscape contexts and histories. To this end, first we generated a current map of woody versus non-woody vegetation, from RapidEye satellite images from 2015 (5 m resolution) using an automatic image classification, based on Maximum Likelihood in ArcGIS. We also determined historical forest cover using supervised image classification of Landsat imagery from 1973 (Landsat 1-MSS, obtained from <http://www.usgs.gov/>).

Then, using the current forest map, we stratified the forest in a way that most likely captured the expected full gradients of forest conditions, especially with respect to human disturbances. Here, we assumed that forest disturbances could be closely related with accessibility, as a proxy for the likely level of human interference – remote sites deep within the forest may be less disturbed than highly accessible areas. Based on this, we stratified the current forest into four cost distance classes (low, medium, high and very high cost distance), using the cost distance analysis tool in ArcGIS, which takes into account the distance to a given point and uses a penalty for steep slopes (which reduce accessibility). Then, we determined the proportion of forest cover and hence, the proportion of cost distance classes within each *kebele* using the above mentioned current land cover map. Finally, we randomly selected a total of 108, 20 m by 20 m sites, distributed across the five *kebeles* (ranging between 9 and 38 sites per *kebele*) and across the four cost distance classes (29 in low, 21 in medium, 20 high, and 38 very high cost distance). In general, such randomly located sites stratified by cost-distance have the advantage of being unbiased by subjective classification (but see Hundera et al., 2013; Tadesse et al., 2014a) and proximity to roads. The disadvantage is that our approach was not fully balanced with respect to other environmental or forest conditions; such as primary versus secondary forests (e.g. we actually got very few interior secondary forests, see below).

2.3. Woody plant surveys

We surveyed woody plants from November 2015 to January 2016, and from April to May 2017. At each of the 108 sites, we recorded all individuals of tree and shrub species with height ≥ 1.5 m. As the existence of young trees is typically correlated with the presence of seedlings (recent regeneration) in a given site (e.g. Fischer et al., 2009), for logistical reasons, we chose not to count individuals < 1.5 m in height for this study. We identified plants that were readily identifiable

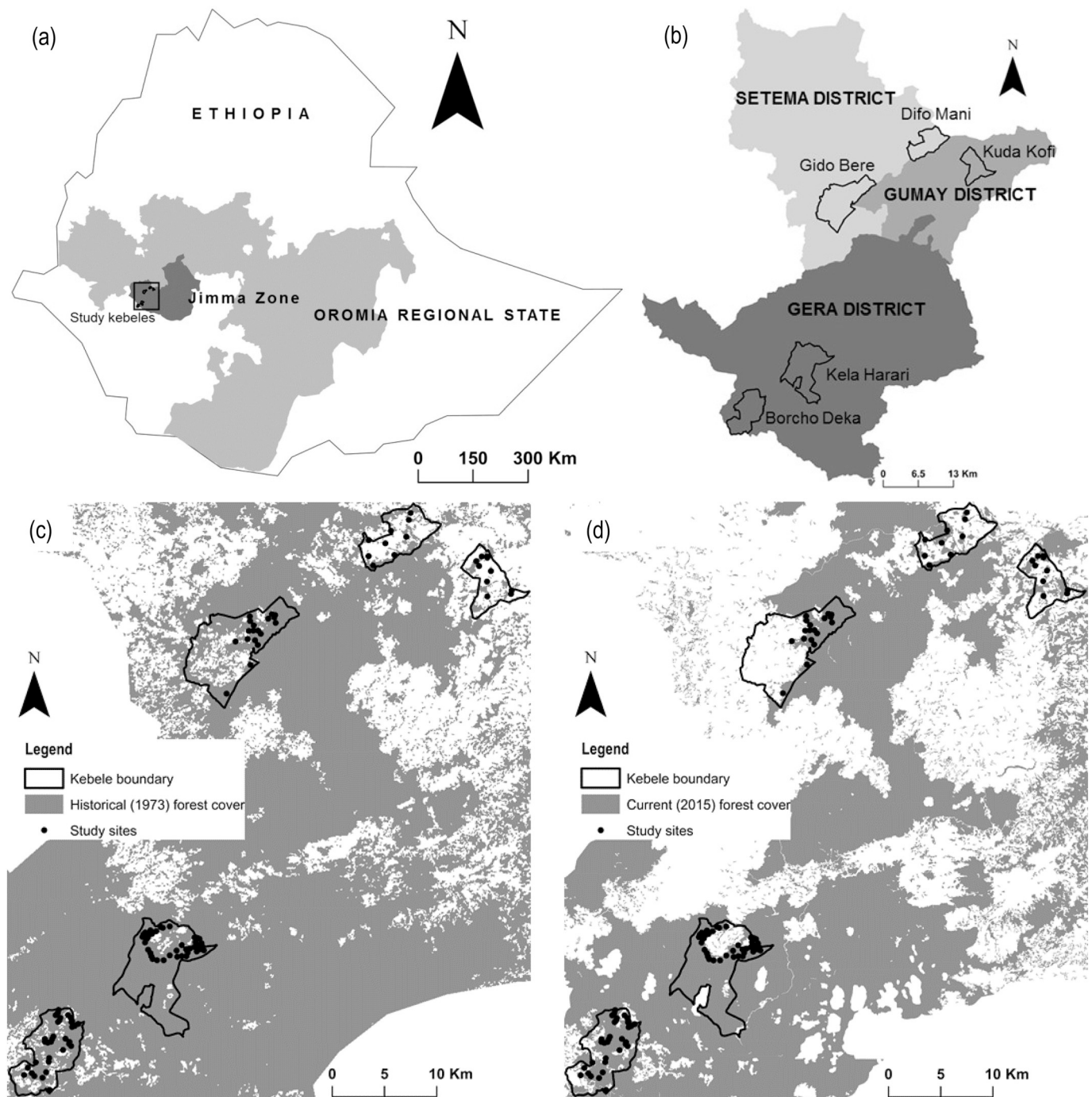


Fig. 1. Overview of (a) location of the study area (square) in Ethiopia; (b) study area with the five study kebeles highlighted; (c) historical (1973) forest cover (grey color) and survey sites (black points); and (d) current (2015) forest cover (grey color) and survey sites (black points).

in the field. For species that were difficult to identify in the field, specimens were collected, pressed, dried and transported to the National Herbarium at Addis Ababa University for identification. Nomenclature followed the *Flora of Ethiopia and Eritrea* (1989–2006). Species were further segregated into forest specialist, generalist and pioneer species (Appendix A) based on relevant literature (*Flora of Ethiopia and Eritrea*, 1989–2006; Teketay, 1997; Tesfaye et al., 2002; Hundera et al., 2013). For each site, we quantified (1) total species richness, (2) forest specialist richness, (3) pioneer species richness, and (4) generalist species richness.

2.4. Forest and environmental parameters

To account for the actual coffee management intensity *in situ* at each site (Fig. 2), we quantified coffee dominance. Coffee dominance was measured as ranging from 0 to 1, and was determined as the ratio of the number of coffee plants to the total number of woody plants in each site (Rodrigues et al., 2018). This measure of coffee dominance was used because it is a countable, objective measure of how many stems of a given site are coffee, out of all stems. In undisturbed or unmanaged coffee forest, coffee plant density is very low, while in



Fig. 2. Overview of forest disturbances and coffee management gradients in southwestern Ethiopia: (a) relatively undisturbed or unmanaged interior coffee forest site; (b) slightly managed interior coffee forest site; (c) managed semi-plantation coffee forest site; and (d) intensively managed semi-plantation coffee forest site.

Table 1

Number of the surveyed 20 m by 20 m sites in terms of forest strata and current Euclidean distance from the nearest forest edge in primary and secondary forests (see Methods for details).

| | Category | Sites in primary forest (forested in both 1973 and 2015) | Sites in secondary forest (forested in 2015, but farmland in 1973) | Total |
|-----------------------------------|---|--|--|-------|
| Forest strata | Low cost distance | 22 | 7 | 29 |
| | Medium cost distance | 19 | 2 | 21 |
| | High cost distance | 18 | 2 | 20 |
| | Very high cost distance | 36 | 2 | 38 |
| | Total | 95 | 13 | |
| Current distance from forest edge | Edge sites (with < 100 m from edge) | 26 | 9 | 35 |
| | Interior sites (with > 100 m from edge) | 69 | 4 | 73 |
| | Total | 95 | 13 | |

intensively managed coffee forest, it is much higher typically and constitutes > 50% of all plants (Schmitt, 2006). The high dominance of coffee in intensively managed sites results from shrub and small tree species other than coffee being systematically removed by coffee growers (Hundera et al., 2013). Low values of “coffee dominance” therefore indicate a high likelihood of coffee occurring at natural densities, while high values of coffee dominance indicate human interference. To account for landscape context as distinct from cost distance (which was used only to guide site selection), we determined the current Euclidean distance of the center of the survey sites from the nearest current forest edge. We also compared the current (2015) forest map with the historical (1973) forest map to classify each site as primary forest (forested in both 1973 and 2015) versus secondary forest (forested in 2015, but farmland in 1973). This way, after our initial site selection, we classified 95 sites as primary forest sites and 13 as secondary forest. A summary of study sites by their cost distance classes and current distances from the nearest forest edge in both primary and secondary forests is provided in Table 1.

Finally, we quantified other environmental variables that we believed might affect woody plant composition and richness as covariates, namely altitude and heat load of the sites. The ASTER Digital Elevation Model (30 m resolution; <https://reverb.echo.nasa.gov/>) was used to derive altitude; heat load was calculated following the procedures described by Olsson et al. (2009). An overview of all variables ultimately used for statistical analysis and their description is provided in Table 2.

2.5. Data analysis

First, we investigated which environmental variables drive community composition. Second, we modelled total species richness, richness of forest specialist, generalist and pioneer species in response to the explanatory variables (Table 2).

Using the log-transformed abundance data of all species (except *Coffea arabica*) in all study sites, we conducted constrained correspondence analysis (CCA) to assess how environmental predictors could explain species composition. We tested if plant community composition and study site scores correlated with coffee dominance, current distance from the forest edge, forest type, heat load, and altitude, using the CCA from the ‘vegan’ package (Oksanen et al., 2018) in R Core Team (2018). Prior to this, we conducted a detrended correspondence analysis (DCA) to determine the length of the compositional gradient, which denotes the degree of species turnover in the community (Hill and Gauch, 1980). All explanatory variables except altitude were log-transformed, and all predictors were tested for significance ($p < 0.05$) using 999 permutations. We specified *kebele* to account for the non-independence of the samples within a *kebele*.

We then used generalized linear mixed effects models (GLMMs) with a Poisson error structure to investigate the effects of local and landscape level explanatory variables (Table 2) on richness of (1) total species, (2) forest specialist species, (3) generalist species and (4) pioneer species. In all cases, we specified *kebele* (to account for grouping in experimental units) and an observation-level dummy variable (to account for overdispersion) as random effects. Prior to modelling, we checked for possible correlations among explanatory variables. Most correlations were below 0.2, but there was a stronger correlation between coffee dominance and altitude (correlation coefficient $r = 0.6$). In this case, we still included both variables in the regression models, but checked that all models had a variance inflation factor of < 2. Furthermore, we log-transformed coffee dominance, current distance to the forest edge, and heat load to remove skew, and scaled all continuous variables to zero mean and unit variance to obtain directly comparable coefficients. Finally, to visualize local and landscape level effects, we predicted species richness in response to coffee dominance and current distance to the forest edge.

Table 2
Definition and description of the explanatory variables used to model plant species richness.

| Type | Variable | Definition and method |
|---------------|------------------|--|
| Fixed effect | Current distance | The distance in m from the center of the site to the nearest current (2015) forest edge (Fig. 1c). |
| | Coffee dominance | The ratio of the number of coffee plants to total number of woody plants in a given site |
| | Altitude | Altitude above sea level derived from the ASTER DEM. |
| | Heat load | Measure of potential incident radiation and temperature, estimated from aspect and slope (Olsson et al., 2009) |
| Random effect | Forest type | Forest land use with two factors – primary forest since 1973 and secondary forest restored after 1973 from farmland. |
| | Kebele | Smallest administrative unit within which sites were nested. |
| | Dummy | Observation level random effect to account for overdispersion. |

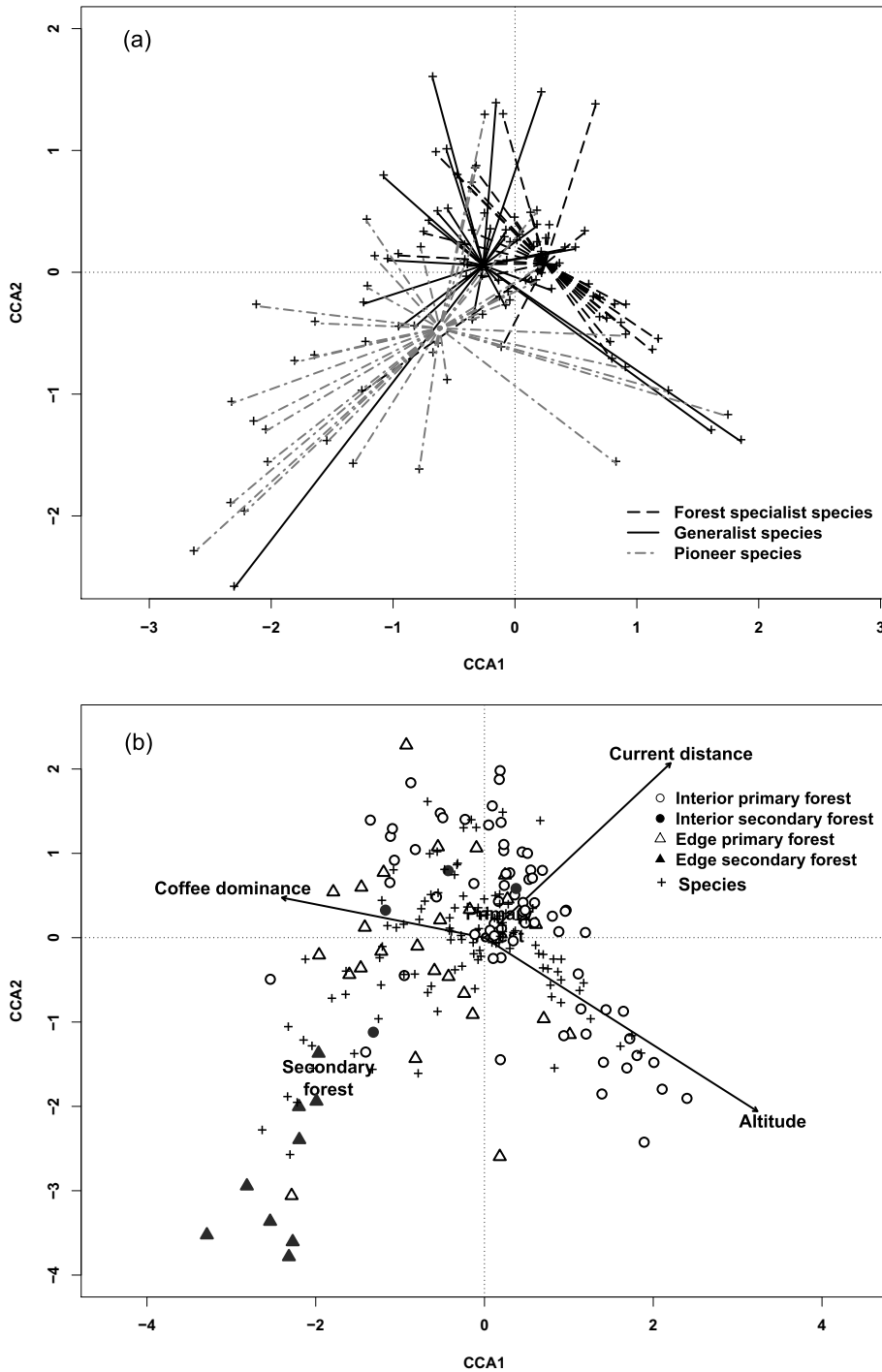


Fig. 3. CCA ordination. (a) CCA biplot showing woody plant species (indicated by “+” sign) (except *Coffea arabica*) based on log-transformed abundance data. Species were grouped and connected to their group’s centroid by lines: forest specialist species (black long-dash lines), generalist species (black lines) and pioneer species (grey two-dash lines). (b) CCA biplot of all 108 study sites (indicated by circles and triangles), all 112 species (except *Coffea arabica*) (indicated by “+” sign) and the significant environmental variables. Study sites were classified by their current distance from the nearest forest edge, with > 100 m edge distance as forest interior sites (circles), and < 100 m edge distance as edge sites (triangles); and also by forest type: primary forest sites (unshaded circles and triangles), and secondary forest sites (black-shaded circles and triangles). Explanatory variables significantly correlated with plant community composition ($p < 0.001$) were altitude, current distance, coffee dominance and forest type- secondary forest.

3. Results

3.1. Species composition analysis

A total of 113 (including one unidentified) species of trees and shrubs, representing 40 families, were recorded from all sites (Appendix A). Of these, 45 were forest specialist, 30 were generalist, and 38 were pioneer (including two planted) species. The most abundant species were *Coffea arabica* (a forest specialist occurring at 78 sites), *Maytenus arbutifolia* (generalist at 64 sites), *Chionanthus mildbraedii* (forest specialist at 55 sites), *Vernonia auriculifera* (pioneer at 50 sites), *Dracaena afromontana* (forest specialist at 37 sites), and *Justicia schimperiana* (generalist at 33 sites) (Appendix A).

The first DCA axis had a length of 3.89 standard deviations, indicating almost a complete species turnover along the main compositional gradient. The CCA ordination indicated that different groups of species occupied different locations but with substantial overlap (Fig. 3a). The CCA showed that woody plant community composition was significantly correlated with several explanatory variables ($F = 2.333$, $p < 0.001$; Fig. 3b). Woody plant community composition was significantly associated with altitude ($F = 4.483$, $p < 0.001$), forest history – secondary forest ($F = 2.342$, $p < 0.001$), coffee dominance ($F = 2.959$, $p < 0.001$) and current distance from forest edge ($F = 2.928$, $p < 0.001$).

3.2. Species richness models

Total species richness and forest specialist species richness were negatively related to coffee dominance (Table 3; Fig. 4a, d). Richness of forest specialist species increased significantly in both primary and secondary forests with current distance from the forest edge (Table 3; Fig. 4e, f), while richness of pioneer species decreased significantly in both primary and secondary forests with current distance from the forest edge (Table 3; Fig. 4h, i). A lower richness of forest specialist species was found in secondary as opposed to primary forest (Table 3; Fig. 4f). In addition, richness of total species was negatively related to

altitude and heat load, and richness of generalists and pioneer species declined with altitude (Table 3).

4. Discussion

Focusing on biodiverse moist evergreen Afromontane forest, we found evidence of site-level disturbance, landscape context, and forest history effects on woody plant species composition and richness. First, we observed significant negative effects of coffee management intensity on total species richness and forest specialist species richness. Second, we identified contrasting landscape context effects, namely a positive effect of distance from the current forest edge on forest specialist species richness, and a negative effect on pioneer species richness. Third, we found significantly lower forest specialist richness in secondary versus primary forest.

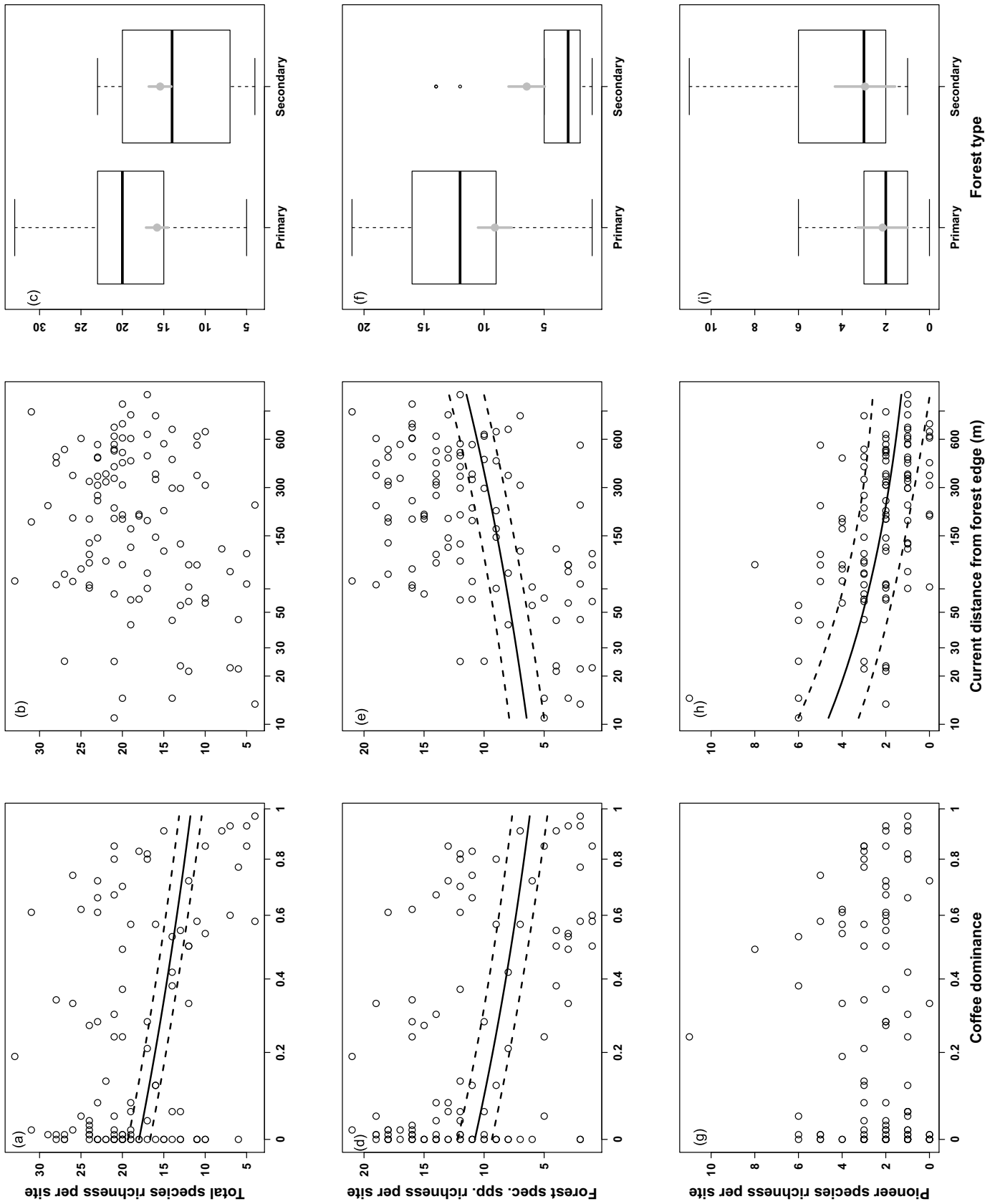
Unlike many other studies in the region (and elsewhere in the tropics) (e.g. Gole, 2003; Hundera et al., 2013; Tadesse et al., 2014a), using a spatially randomized design based on cost distance and a large data set, we were able to cover large gradients of forest conditions in relation to coffee management, landscape context and forest history. Our findings revealed independent effects of all three gradients, highlighting the importance of their recognition in developing appropriate conservation strategies. We discuss these findings and their implications for conservation in relation to other studies, particularly from Ethiopia and other tropical regions.

The merit of shade coffee systems for biodiversity conservation and ecosystem services has received considerable attention globally (Jha et al., 2014; Tadesse et al., 2014a; Rodrigues et al., 2018). Coffee is grown across southwestern Ethiopia (Senbeta and Denich, 2006; Schmitt et al., 2010; Hundera et al., 2013) as well as in Latin America and elsewhere in the tropics (Perfecto et al., 1996; Philpott and Dietsch, 2003; Hernández-Martínez et al., 2009), often under the shade of native trees. However, a major difference in Ethiopia is that Arabica coffee is a native, primary component of forest ecosystems (Schmitt, 2006; Aerts et al., 2011). Here, traditional coffee management intensity ranges from very low disturbance forest systems to semi-plantation systems

Table 3

Results of generalized linear mixed effects models for total species richness, forest specialist species richness, pioneer species richness and generalist species richness. Explanatory variables were continuous except for forest type. The coefficient for forest type indicates the difference between primary and secondary forest, with primary forest being the reference level. Significance levels are indicated by: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

| Response | Term | Coefficient | Standard error | Z-value | P-value |
|------------------------------------|------------------|-------------|----------------|---------|-------------|
| Total species richness | Intercept | 2.761 | 0.142 | 19.485 | < 0.001 *** |
| | Current distance | -0.000 | 0.031 | -0.009 | 0.993 |
| | Coffee dominance | -0.148 | 0.038 | -3.908 | < 0.001 *** |
| | Heat load | -0.065 | 0.028 | -2.284 | 0.022 * |
| | Altitude | -0.145 | 0.046 | -3.188 | 0.001 ** |
| | Forest type | -0.024 | 0.110 | -0.220 | 0.826 |
| | Intercept | 2.209 | 0.171 | 12.924 | < 0.001 *** |
| Forest specialist species richness | Current distance | 0.137 | 0.043 | 3.220 | 0.001 ** |
| | Coffee dominance | -0.193 | 0.051 | -3.766 | < 0.001 *** |
| | Heat load | -0.058 | 0.036 | -1.609 | 0.108 |
| | Altitude | -0.088 | 0.060 | -1.466 | 0.143 |
| | Forest type | -0.344 | 0.167 | -2.067 | 0.039 * |
| | Intercept | 0.765 | 0.071 | 10.774 | < 0.001 *** |
| | Current distance | -0.305 | 0.063 | -4.825 | < 0.001 *** |
| Pioneer species richness | Coffee dominance | -0.146 | 0.079 | -1.849 | 0.065 |
| | Heat load | -0.024 | 0.063 | -0.372 | 0.710 |
| | Altitude | -0.163 | 0.082 | -1.971 | 0.049 * |
| | Forest type | 0.318 | 0.176 | 1.812 | 0.070 |
| | Intercept | 1.377 | 0.203 | 6.780 | < 0.001 *** |
| | Current distance | -0.087 | 0.049 | -1.772 | 0.076 |
| | Coffee dominance | -0.046 | 0.059 | -0.782 | 0.434 |
| Generalist species richness | Heat load | -0.065 | 0.052 | -1.252 | 0.211 |
| | Altitude | -0.260 | 0.078 | -3.356 | < 0.001 *** |
| | Forest type | 0.029 | 0.177 | 0.163 | 0.871 |



(caption on next page)

Fig. 4. Effects of coffee management, current distance from nearest forest edge, and forest type on richness of total species (panels (a), (b) and (c)), forest specialist species (panels (d), (e) and (f)), and pioneer species (panels (g), (h) and (i)) based on the generalized linear mixed effects models. Solid black regression lines indicate model predictions for primary forest while all other variables were held constant at their means; and dashed lines indicate 95% confidence intervals. The x-axes display original values but both coffee dominance and current distances were scaled and used on a logarithmic scale in the models. The box-and-whisker plots (c, f, i) illustrate the relationship between forest type and species richness, where the grey dot represents the predicted means and the grey lines the corresponding 95% confidence intervals.

(Teketay, 1999; Wiersum et al., 2008; Tadesse et al., 2014a). Our findings revealed negative effects of intensively managed coffee systems on native species composition and diversity as opposed to undisturbed coffee forest sites. Several native tree species, such as *Cassipourea malosana*, *Chionanthus mildbraedii*, *Pouteria adolfi-friederici*, and *Trichilia dregeana* appeared to be affected by intensive coffee management. This is consistent with other studies in southwestern Ethiopia, which also found strong negative effects on native plant species (Gole, 2003; Schmitt et al., 2010; Hundera et al., 2013) and on forest and dietary specialist birds (Gove et al., 2008; Rodrigues et al., 2018), suggesting loss and homogenization of biodiversity in increasingly simplified forest coffee systems.

At a landscape level, edge effects are known to have negative consequences on native forest species (Murcia, 1995; Gascon et al., 2000; Wiens, 2002). However, landscape context and site effects are often confounded and therefore usually difficult to differentiate in their respective influences on biodiversity (Harper et al., 2005). Here, we found edge-mediated landscape effects on species composition and richness that were not related to coffee management. Our findings show that sites closer to the forest edge differ in native species composition from sites in the interior forest. Of the forest specialist species, for example, *Chionanthus mildbraedii*, *Pouteria adolfi-friederici*, *Podocarpus falcatus*, and *Schefflera abyssinica* appeared to be most strongly affected by edge effects. Furthermore, edge influence extended relatively deep into the forest, with forest species richness continuously increasing deep into the forest, strongly affecting up to 100 m from the edge but potentially reaching several hundred metres into the forest (Fig. 4e). Our empirical findings are consistent with earlier southwestern Ethiopian studies that showed forest and dietary specialist bird species diversity (Rodrigues et al., 2018) and understory epiphytic fern and epiphyllous bryophyte cover (Hylander et al., 2013b) to increase towards the interior of the forest. As to the distance of edge influence, the edge effect in our study area was comparable to edge effects reported elsewhere in the tropics (Harper et al., 2005), such as 100 to 300 m in central Amazonian lowland rainforest (Laurance et al., 1998) and 500 m in tropical forest in Queensland, Australia (Laurance, 1991). A possible driver for the edge effects in our study area may be the relatively intensive use of forest edges by local people, which includes but is not restricted to coffee growing. Local people in the region greatly depend on wood and non-wood forest products such as fuelwood, construction materials including poles and timber, farm and household tools, and honey (Ango, 2016; Dorresteijn et al., 2017). While forest edges may be hotspots of such human uses, people in the region further penetrate the forest to find and use resources from considerable distances (Hylander et al., 2013b), thereby potentially causing far-reaching edge effects (Didham and Lawton, 1999; Gascon et al., 2000; Cadenasso et al., 2003). These findings highlight the general importance of maintaining largely undisturbed forest interior locations for native species conservation (Gibson et al., 2011; Barlow et al., 2007).

Secondary forests in our study area hosted significantly lower forest specialist species richness and differed in composition compared to primary, old-growth forests. At the species level, for example, *Cassipourea malosana* and *Trichilia dregeana* did not occur at secondary forest sites, and *Pouteria adolfi-friederici* and *Syzygium guineense* occurred at only one interior secondary forest site (noting that we had only four interior sites of secondary forest in total). Such decreases in native tree species richness in secondary forest have been noted consistently in the tropics (Chazdon, 2003; Lugo and Helmer, 2004; Wright, 2005). Possible reasons for lower native tree species richness in

secondary forest are land use legacy effects of past agricultural land use (e.g. loss of individual trees or propagules, habitat change, inadequate seed dispersal, or loss of soil fertility; Shumi et al., 2018; Thompson et al., 2002; Arroyo-Rodríguez et al., 2017) coupled with the inherently slow natural restoration and restocking with slow-growing tree species. Our findings demonstrate that secondary forests, which we also found to differ in species composition from primary forests, may take up to 40 years (assuming that the oldest regrowth could have occurred immediately after 1973) and longer to attain a similar composition to remnant forest. This matches closely with other forest ecosystems, where recovery in species composition takes several decades – e.g. 30–40 years in Atlantic secondary forest in southern Brazil (Zanini et al., 2014), 80 years in south-eastern Puerto Rico (Marin-Spiotta et al., 2007), and 70–100 years in central Panama (DeWalt et al., 2003). Overall, while our results clearly underline the primary importance of safeguarding old growth native forests (see Gibson et al., 2011; Barlow et al., 2007), they also highlight the need for assisted and natural recovery of forests (Chazdon, 2008; Crouzeilles et al., 2017).

4.1. Conservation implications

Our study revealed a combination of site-level, historical and landscape-level effects on Ethiopian forest biodiversity. Because coffee is important for local livelihoods and Ethiopia's economy (Petit, 2007; Moat et al., 2017), pressure on forest biodiversity from coffee management intensification is potentially high (e.g. Hundera et al., 2013; Tadesse et al., 2014a). Further forest degradation could also result from an increasing number of local people heavily depending on forest products (Ango, 2016; Dorresteijn et al., 2017). Moreover, imperfect forest management and investment policies, and poorly defined property rights (e.g. Lemenih and Kassa, 2014; Tura, 2018) have also exposed Ethiopian forests to recurrent deforestation (e.g. Tadesse et al., 2014b; Getahun et al., 2017), particularly in areas above coffee altitude (e.g. Hylander et al., 2013a).

Biodiversity conservation in southwestern Ethiopia and similar systems elsewhere requires integrated strategies that foster appropriate local and forest landscape management (Gardner et al., 2009; Edwards, 2016; Chazdon, 2018). One option could be to further promote the biosphere reserve approach, which can integrate sustainable development and biodiversity conservation (Batisse, 1982; Bridgewater, 2002). Eco-friendly coffee certification schemes could additionally help to maintain specialist species in managed coffee forests (Perfecto et al., 2005; Takahashi and Todo, 2017). Given the high dependence of local livelihoods on forest products and the vulnerable biodiversity in southwestern Ethiopia, however, any approach must carefully weigh social and ecological costs and benefits.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2019.02.008>.

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