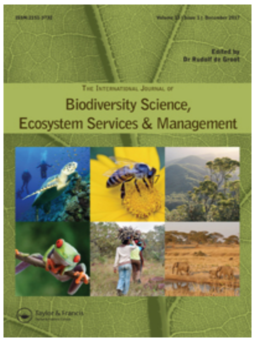

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Effects of biodiversity loss and restoration scenarios on tree-related ecosystem services

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ABSTRACT

In landscapes worldwide, trees in forests and agricultural lands have important ecological functions. Their loss may have important consequences for the delivery of ecosystem services (ES) to local communities, even if individual trees have low conservation values. This study explores the effect of land use and land use change on the provisioning of tree-related ES in a mixed Afromontane landscape in Ethiopia. First, we mapped the current distribution of tree-related ES using indicator ES, which represent the most characteristic ES for different land use types. More ES were characteristic for indigenous forest and agroforest, compared to exotic forest, cropland, and rangeland. A scenario analysis was conducted on the effect of tree species loss and restoration (RES) on ES. Two ES indices, ES diversity and ES multifunctionality, were used to evaluate the ES supply. The different behavior of the two ES indices in the species loss scenarios suggests that rare species have distinct traits that provide specific ES, which could not be compensated by the remaining common species. In tree species-poor landscapes, local communities prefer multifunctional tree species and these keep the diversity of ES supply high. Overall, our findings demonstrate that future conservation and restoration programs in mixed landscapes should both protect a large diversity of tree species, including rare tree species, and promote multifunctional keyston species to ensure a long-term and diverse ES supply.

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1. Introduction

In many regions worldwide, forests are surrounded by landscapes of mixed land uses, including those with isolated trees or trees occurring scattered in groups, either remaining from the original forest or newly planted (Manning et al. 2006; Herrera and García 2009). While forest ecosystems are well known for supporting higher tree coverage, it is less known that 43% of global agricultural land had at least 10% tree cover (Zomer et al. 2016). Both in the forests and the surrounding agricultural landscape matrix, trees may be threatened by human interventions such as agricultural expansion or intensification (INT), and destructive forms of fuelwood or timber harvesting (Hartter 2010). As these trees fulfill key ecosystem functions, their loss may have important consequences for ecosystem services (ES) provided to local communities. Understanding of the role of species diversity in ecosystem functioning is improving (Cardinale et al. 2012; Mace et al. 2012). Many studies have reported a positive relationship between species richness and ES (Harrison et al. 2014). A particular observation is that ES are usually delivered by a few dominant species (Schwartz et al. 2000; Lawler et al. 2001), so there is growing consensus that a certain level of biodiversity must be conserved to maintain ES, but that the role of rare species is limited. However, insights about the effects of biodiversity on the functioning of terrestrial ecosystems are mainly deduced from grassland experiments, as these are easy and fast to establish (Nadrowski et al. 2010). Less attention has been paid to such effects in forest and agricultural ecosystems. In addition, in biodiversity-ecosystem function (BEF) experiments, species richness is controlled artificially using randomly assembled communities. Yet these synthetic communities usually do not provide realistic scenarios of biodiversity loss (Duffy et al. 2009). Hence, our understanding of how nonrandom species loss affects ecosystems functions is limited (Balvanera et al. 2014). In recent years, the focus of BEF research has shifted from single ecosystem function to ecosystem multifunctionality (MF), which is the ability to maintain multiple ecosystem functions at high levels

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simultaneously (Byrnes et al. 2014). New MF indices summarize the overall performance of an ecosystem in simple metrics (e.g. Maestre et al. 2012). This shift in focus has resulted in new insights into the BEF relationship at landscape scale. The importance of biodiversity for the functioning of ecosystems increases when considering multiple ecosystem functions due to the complementarity of different species (Gamfeldt et al. 2008).

A case study was conducted in Menagesha Suba Forest and the surrounding agricultural landscape in the central highlands of Ethiopia, where the region is characterized by long-term social–ecological interactions between the forest and its neighboring villages (Duguma et al. 2009). The first goal of this study was to map the current distribution of tree-related ES. We inventoried tree species composition along a land use intensity gradient from indigenous forest (IF) (low land use intensity) to agricultural land uses (high land use intensity) and identified the current ES supported by all occurring tree species. To see whether certain tree-related ES were bound to specific land use types, we performed an indicator ES (IES) analysis. While the original indicator species analysis of Dufrêne and Legendre (1997) was meant to identify characteristic species for a given plant community, we used it here to identify characteristic ES for a given land use type.

Our second goal was to assess the effects of species loss and gain on the provision of tree-related ES in this mixed landscape. For this second goal, we evaluated the response of two ES indices to different scenarios of species loss and landscape restoration (RES). We used the combination of two indices, ES diversity (ESD) (Laliberté and Legendre 2010), and ESMF (Byrnes et al. 2014), each highlighting different aspects of ES supply in the landscape. This allowed us to gain new insights into the relationship between biodiversity and ES provision and the distribution of ES at landscape scale.

2. Materials and methods

2.1 Study site

Our study site was the Menagesha Suba Forest and the surrounding agricultural landscape (8°53′24″ – 9°03′0″ N and 38°27′36″ – 38°39′36″ E) located in the central highlands of Ethiopia (Figure 1). Menagesha Suba Forest is a unique example of early conservation in Africa, protected since the sixteenth century after it was replanted with *Juniperus procera* Hochst. ex Endl. trees as a royal forest of King Zera Yakob (1597–1603). The vegetation is predominantly indigenous conifers and hardwoods (Gelet et al. 2010), and is classified as undifferentiated Afromontane forests dominated by *J. procera* (sensu Friis 1992). After forest loss during the twentieth century, forest cover expanded due to exotic tree plantations following the 1975 land policy reform, attaining about 3500 ha (Bekele, 2003). Currently, the forest is surrounded by an agricultural mosaic landscape with different

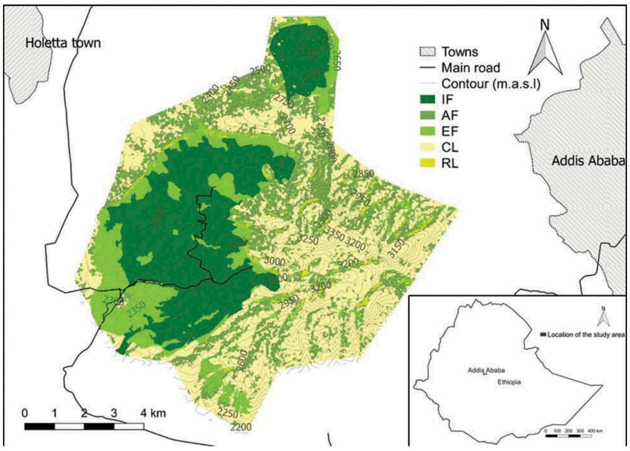

Figure 1. Location of the study area, showing spatial distribution of the major land use types in the landscape: indigenous forest (IF), agroforest (AF), exotic forest (EF), cropland (CL), and rangeland (RL).

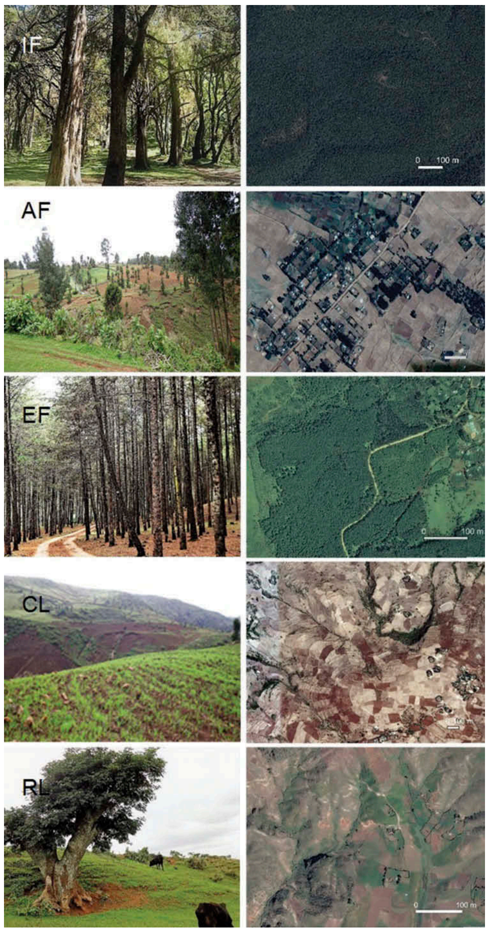

Figure 2. Illustration of the land use types: Photograph (2015, left) and satellite images (right) (Satellite image © 2015 CNES/Astrium – Google Earth) of indigenous forest (IF), agroforest (AF), exotic forest (EF), cropland (CL), and rangeland (RL).

land use types, mainly agroforestry, cropland (CL), and rangeland (RL) (Figures 1 and 2).

2.2 Data collection

Within the study area, we established 85 plots (25 × 25 m^2) with a stratified random sampling of five land use types: IF (= 30 plots), EF (= 15 plots), AF (= 15 plots), CL (= 15 plots), and RL (= 10 plots) (Figure 2). In each plot, the altitude and slope were recorded. Soil was sampled at 0–10 cm depth in the four corners of each plot and these samples were combined per plot. In total, 85 topsoil samples (0–10 cm depth) were collected and analyzed for soil organic carbon (SOC), total nitrogen, and pH. For estimation of soil bulk density, undisturbed soil samples were taken from the same depth using a soil core sampler. The altitude, slope, and results of soil analysis were only used to describe the physical characteristics of the studied land use types. Total height and diameter at breast height (DBH) of all trees and shrubs above 5 cm DBH were measured in the plots. Tree species identification and nomenclature followed the Flora of Ethiopia and Eritrea (Edwards et al. 2000).

2.3 Tree-related ES

All observed tree species were scored for their potential ES provision. Two approaches were combined to obtain a species-specific score for each ES. First, we performed a literature search on the selected species (Bekele 2007; Alajmi and Alam 2014; Seyoum et al. 2015) and second, we conducted focus group discussions with selected key informants of the community living in the study area. Based on these discussions, each species was scored for each ES, according to local knowledge and habits. Then, both information sources were combined to one score as follows: for a given tree species, a score of 0 was given if the species does not supply a given ES, a score of 1 if the species supplies the ES according to literature, and a score of 2 if the species is actively used for this ES by the local communities in the area. In total, 24 tree-related ES were identified, scored, and used for further analysis.

2.4 Data analysis

2.4.1 Tree species diversity and indicator ES

Prior to analysis, three plots, two from the EF and one from AF were removed as outliers, by using a cutoff point of two standard deviations from the grand mean Sørensen distance. Ten more plots were excluded from CL and RL due to very low or zero tree occurrence, which reduced the total evaluated sample size from 85 to 72 plots. Several diversity indices, i.e. alpha (α), beta (β), gamma (γ), Shannon diversity (H), Simpson diversity (D), and Simpson evenness (E) were calculated to quantify tree species diversity, all based on the basal area data. The α-diversity (local diversity) was defined as the number of species per plot (Whittaker 1972). The γ-diversity was considered as the total number of species found in each land use type (Whittaker 1972). The β-diversity index was defined as γ/α (Whittaker 1972) and indicates species variability within a land use type. To test for significant differences in tree species diversity measures between land use types, Kruskal–Wallis tests and Dunn's *post hoc* tests with Bonferroni correction were performed with the FSA package (Ogle 2016) in R 3.2.5 (R Core Team 2016).

A matrix of plot-specific ES values was obtained by the cumulative weighted average calculation of the species × plot matrix with the species × ES matrix, which was composed by scoring ES for each tree species. The outcome of this operation was an ES × plot matrix, i.e. a matrix with ES values for each plot across the land use types. The ES values were then used for (i) ordination to see the association of tree-related ES with each land use types by means of principal component analysis (PCA) using PC-ORD 5.0 for Windows (McCune and Mefford 1999) and (ii) the calculation of IES according to the indicator species analysis procedure of Dufrêne and Legendre (1997).

Indicator species analysis is based on the relative frequency of species and concentration of abundance within particular groups. The Dufrêne and Legendre (1997) method calculates indicator species by assigning an indicator value (IV) index between a species and each group, identifying the group with the highest association value, and using a randomization procedure to test the statistical significance of this value. Analogously, we applied indicator species analysis to ES (instead of species) to calculate IES using the plot × ES matrix and land use types as a vector criterion.

2.4.2 Scenario analysis

Five scenarios were modeled and compared to the current situation (CS); four scenarios simulated species loss: business as usual (BAU), extinction (EXT), land use INT (LUI), and deforestation (DEF), and one scenario simulated RES. In BAU, the forest, even if protected, continues to undergo a gradual degradation process due to population pressure. The current forest conservation strategy mainly focuses on maintaining economically important indigenous and exotic tree species. The EXT scenario is defined as the extreme case of the BAU scenario, where completely neglecting the protection of less important tree species results in losing all uncommon species. Stricter conservation of the forest in LUI causes pressure on trees outside the forest leading to conversion of agroforestry land with high tree cover to CL with low tree cover. Increased population pressure in combination with failing conservation efforts would lead to agricultural expansion into the IF, which is the rationale for the DEF scenario. In the only RES scenario, the landscape is rehabilitated by tree planting in the IF and in the agricultural land use types. The detailed description of all scenarios and the methodological approach for each scenario in terms of transformations of the basal area matrix is given in supplementary material (Table S1).

Using the scenario analysis, we investigated the effects of species loss and RES on ESD and ESMF. ESD was quantified using the functional dispersion index (FDis) of Laliberté and Legendre (2010), which is a measure of the dispersion of species in the trait space. FDis is calculated as the average distance of all species to their centroid. We use it here for the first time in a context of ES. ESD is thus an indicator of the dispersion of the tree species in the ES space and takes into account the occurrence of the ES in the landscape. ESD was calculated with the FD package (Laliberté and Legendre 2010) in R 3.2.5.

ESMF is the ability to maintain multiple ecosystems services at high levels simultaneously (reviewed by Byrnes et al. 2014, in a context of ecosystem functions), but does not make a distinction between rare and abundant ES. We used an averaging approach to estimate ESMF, which involved averaging standardized values of multiple services into a single index. First, we calculated the community-weighted means (CWM) of each ES per plot (Maestre et al. 2012), after standardizing the CWM values by the maximum, as recommended by Byrnes et al. (2014). The values of ESMF per plot were calculated by averaging over all ES. Once calculated, we compared the relative changes of ESD and ESMF values between the CS and each of the scenarios using a Dunnett's tests with the multcomp package (Hothorn et al. 2008) in R. The direct relationship between species richness and ESD as well as ESMF in all species loss and RES scenarios was evaluated by fitting linear regression models.

3. Results

3.1 Biophysical characteristics of the land use types

The study landscape included forest and agricultural land uses (Figure 2). Forest covered 25% of the total study area, of which 17% was IF and 8% was EF. The agricultural land use covered 75%, of which 26%, 45%, and 4% were AF, CL, and RL, respectively. The IF was located at higher altitude (χ^2 = 22.56, $P < 0.001$) and had a soil characterized by higher SOC (χ^2 = 27.95, $P < 0.001$), and total nitrogen (χ^2 = 32.50, $P < 0.001$), yet lower soil pH (χ^2 = 15.83, P = 0.003), and lower bulk density (χ^2 = 21.80, $P < 0.001$) than AF, EF, CL, and RL (Table 1). The AF, EF, CL, and RL land use types occurred around the IF at a relatively lower altitude and did not significantly differ from each other in altitude, SOC, N, and BD. We found no significant difference in slope between the land use types (χ^2 = 7.04, P = 0.134) (Table 1). In total, 52 tree species were identified in these landscapes (Table S2): 71.2% of this species pool occurred in IF, 13.5% in EF, 40.4% in AF, 23.1% in CL, and 11.5% in RL. The IF was mainly composed of indigenous tree species (89.2%) and had higher γ-diversity than all other land use types: γ-diversity (χ^2 = 71.00, $P < 0.00$) (Table 1). Yet, the IF and AF had significantly higher α (χ^2 = 42.71, $P < 0.001$) and H (χ^2 = 29.90, $P < 0.001$) diversity indices than the other land use types (EF, CL, and RL). Simpson (D) diversity was highest for the AF land use type D (χ^2 = 25.27, $P < 0.001$). The EF, CL, and RL land use types were represented by a low tree species richness dominated by exotics (67.3% exotics in EF, 58.3% in CL and 33.3% in RL). While the CL had the highest tree species variability, i.e. highest β (χ^2 = 22.66, $P < 0.001$) diversity, the RL presented the most uneven distribution of tree species in the landscape: E (χ^2 = 20.71, $P < 0.001$).

3.2 Tree-related IES of land use types

The PCA ordination (Figure 3), with 61.1% of the cumulative explained variance by the first two axes, revealed that ES were distinctly associated with land use types. For the IF, 40.5% of the variance was correlated with the first axis (PCA 1). ES of the remaining land use types (AF, EF, CL, and RL) were explained by 20.6% of variance and associated with the second axis (PCA 2). Overall, the ordination clearly separated ES of the IF from the ES of the human-modified land use types (AF, EF, CL, and RL) along one axis and ES of the other land use types on the second axis. IES were clearly associated with the five land use types, as shown in Table 2. IF had the highest proportion of IES (40% of all identified IES) and is the unique provider of provisioning services such as milk flavoring (IV = 67.1, $P < 0.001$), toothbrushes (IV = 58.1, $P < 0.001$), farm implement materials (IV = 47.6, $P < 0.001$), fuelwood (IV = 23.8, $P < 0.001$), and charcoal (IV = 31.2, $P < 0.001$). The AF, which contained 30% of all IES identified, was important in supplying livestock shade (IV = 69.4, $P < 0.001$), economically important trees (IV = 53.8, $P < 0.001$), edible fruits (IV = 44.5, P = 0.01), nitrogen-fixing trees (IV = 36.8, P = 0.008), and other services. The EF was associated with less IES (20%), mainly provisioning and regulating services, including ornamental trees (IV = 34.2, $P < 0.001$), timber (IV = 30.8, $P < 0.001$), live fences (IV = 30.8, $P < 0.001$), and erosion control (IV = 26.6, $P < 0.001$). The CL and RL land use type represented together only 10% of all IES found on the land use

Table 1. Comparison of the five land use types in terms of physical site characteristics and tree diversity indices (mean ± SE).

	Indigenous forest	Agroforest	Exotic forest	Cropland	Rangeland
	n = 30	*n* = 15	*n* = 15	*n* = 15	*n* = 10
Physical site characteristics					
Elevation (m.a.s.l)*	2600 ± 264^{a}	2470 ± 298^{b}	2382 ± 86^{b}	2427 ± 139^{b}	2396 ± 280^{b}
Slope (%)	8.5 ± 7.0	7.8 ± 10.7	6.5 ± 2.7	13.3 ± 3.6	7.00 ± 3.4
SOC (mass %)*	4.3 ± 0.8^{a}	2.2 ± 0.5^{b}	3.1 ± 1.3^{ab}	1.8 ± 1.8^{b}	2.6 ± 0.9^{ab}
Total nitrogen (mass %)*	0.47 ± 0.05^{a}	0.19 ± 0.04^{b}	0.28 ± 0.10^{ab}	0.17 ± 0.27^{b}	0.23 ± 0.07^{ab}
pH –H_2O*	6.51 ± 0.41^{a}	5.87 ± 0.37^{b}	6.32 ± 0.50^{ab}	5.80 ± 0.66^{b}	6.06 ± 0.51^{ab}
Soil bulk density (g/cm^3)*	1.01 ± 0.14^{a}	1.21 ± 0.11^{b}	1.18 ± 0.21^{b}	1.33 ± 0.26^{b}	1.25 ± 0.08^{b}
Tree diversity indices					
Alpha diversity*	6.5 ± 2.1^{a}	6.8 ± 1.5^{a}	2.1 ± 1.5^{b}	2.3 ± 2.2^{b}	2.3 ± 0.8^{b}
Beta diversity*	6.4 ± 2.1^{a}	3.6 ± 4.4^{b}	4.7 ± 2.3^{ab}	7.5 ± 2.5^{ab}	3.0 ± 1.6^{b}
Gamma diversity*	37	21	7	12	6
H (Shannon diversity)*	0.91 ± 0.42^{a}	1.28 ± 0.50^{a}	0.26 ± 0.37^{b}	0.47 ± 0.43^{bc}	0.62 ± 0.36^{bc}
D (Simpsondiversity)*	0.44 ± 0.19^{ac}	0.61 ± 0.28^{a}	0.14 ± 0.20^{b}	0.26 ± 0.21^{bc}	0.38 ± 0.22^{abc}
E (Simpsonevenness)*	0.49 ± 0.17^{a}	0.68 ± 0.20^{b}	0.44 ± 0.21^{ab}	0.73 ± 0.18^{bc}	0.79 ± 0.12^{c}

Notes: Soil properties are measured from 0 to 10 cm depth. Different letters indicate significant differences between the five land use types following Kruskal–Wallis tests and Dunn's *post hoc* tests with Bonferroni correction. *N* is number of plots per land use type.*P-value of Kruskal–Wallis test <0.05.

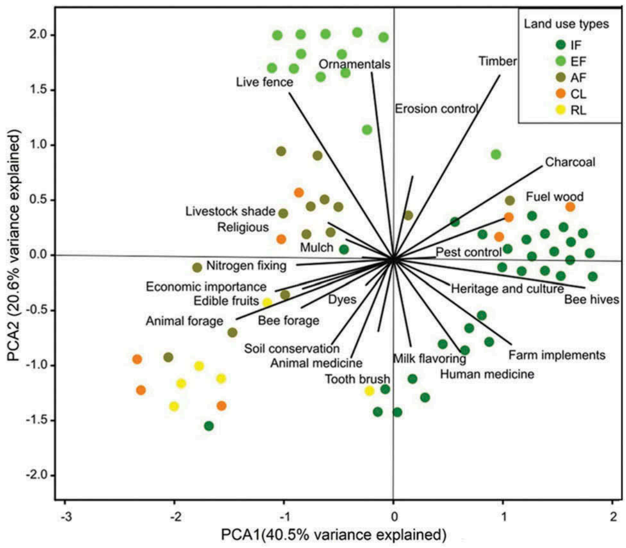

Figure 3. Principal component analysis of ecosystem services provided by trees recorded in 72 25 × 25 m^2 plots in five land use types: indigenous forest (IF), agroforest (AF), exotic forest (EF), cropland (CL), and rangeland (RL).

types. The CL was useful for soil erosion control (IV = 36.9, P = 0.03) and the RL for animal forage (IV = 34.9, P = 0.04) (Table 2, Figure 3).

3.3 Tree species loss and RES scenarios

Compared to the current land use scenario (CS), possible future degradation scenarios resulted in loss of 42.3% of the original tree abundance in BAU, 61.5% in EXT, 11.5% in INT, and 46.2% in DEF scenarios. In the RES scenario, the planting of rare species from the present species pool in IF, CL, and RL land use types (see Table S2) increased the average basal area by 32.7%. In the CS, tree-related ESD and ESMF significantly (α = 0.05) differed between the land use types (Figure 4). Average ESD was highest for IF (4.45), and lowest for EF (0.92) (χ^2 = 26.35, P < 0.001), whereas ESMF was highest for IF (0.30) and lowest for RL (0.15), (χ^2 = 25.77 and P < 0.001) (Figure 5). In the simulations, ESD declined in response to many of the species loss scenarios, while ESMF showed a different trend (Figure 5). Loss and RES of tree species almost did not influence the relationship between species richness and ESD or ESMF (Fig. S1 and S2). Species richness had a significant positive effect on ESD in all species loss and RES scenarios and explained 32–59% of the observed variation in ESD. In contrast, only 0–17% of the variation in ESMF was explained by species richness.

The relative ESD loss from the IF was 3% in BAU and 6% in EXT scenarios compared to the ESD of the CS. It seems that the ESD of the agricultural land use types (AF, CL, and RL) was considerably affected by the loss of rare species. The AF lost 2% and a

Table 2. Overview of the indicator ecosystem services (IES) of the five land use types.

Land use types	Indigenous forest	Agroforest	Exotic tree species forest	Cropland	Rangeland
	Milk flavoring (67.1)	Livestock shade (69.4)	Ornamental (34.2)	Soil conservation (36.9)	Animal forage (29.7)
	Toothbrush (58.1)	Economic importance (53.8)	Live fence (30.8)		
	Heritage and culture (48.6)	Edible fruits (44.5)	Timber (30.8)		
	Farm implements (47.6)	Mulch (36.8)	Erosion control (26.6)		
	Beehive (47.5)	Nitrogen fixing (36.8)			
	Charcoal (31.2)	Bee forage (35.6)			
	Human medicine (30.9)				
	Fuelwood (23.8)				
Proportion of IES	40%	30%	20%	5%	5%

Indicator values (between parentheses) indicate association of an ecosystem service with a specific land use and range from 0 (no indicator) to 100 (perfect indicator). In the table, only significant IES ($\alpha < 0.05$) are presented. *P*-Values are calculated with Monte Carlo permutation tests.

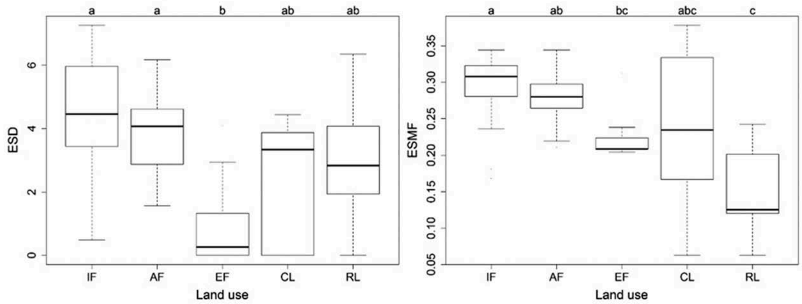

Figure 4. Ecosystem diversity (ESD) and multifunctionality (ESMF) in five land use types: indigenous forest (IF), agroforest (AF), exotic forest (EF), cropland (CL), and rangeland (RL). ESD and ESMF are compared between the current land use types with Kruskal–Wallis tests and the Dunn's *post hoc* tests with Bonferroni correction.

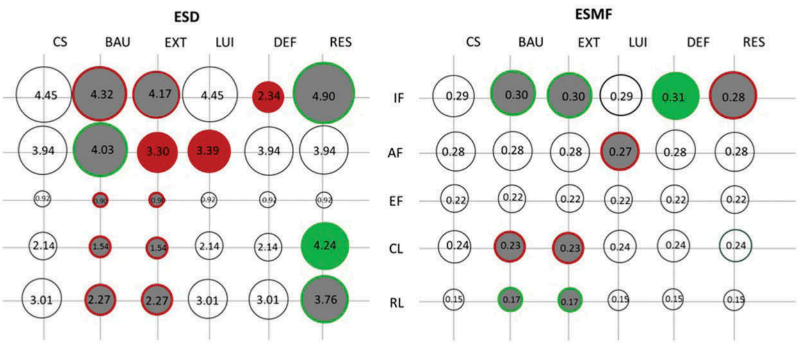

Figure 5. Values of ES diversity (ESD) and multifunctionality (ESMF) in the land use types, as calculated in the scenario analysis. The horizontal axis represents the five land use scenarios: current situation (CS), business as usual (BAU), extinction (EXT), intensification (LUI), deforestation (DEF), and restoration (RES). The vertical axis shows the land use types: indigenous forest (IF), agroforest (AF), exotic forest (EF), cropland (CL), and rangeland (RL). The dimension of the bubbles (and the numbers) corresponds to the values of ESD and ESMF. Bubbles indicate no (white), significant(solid) changes compared to the CS. Comparisons with the CS were performed with a Dunnett's test ($\alpha = 0.05$).

significant loss of 28% of its CS ESD in the BAU and EXT scenarios, respectively, while the CL and RL lost 28% and 25% of their CS ESD each in the BAU and EXT scenarios, respectively. The EF was the least affected, losing 2% of its CS ESD as a result of species loss in BAU and EXT scenarios. Species loss because of the conversion of (i) AF and (ii) IF to CL in (i) LUI and (ii) DEF scenarios resulted in significant losses of ESD, i.e. (i) 14% and (ii) 47%, respectively. Planting less represented species in the RES scenario significantly increased the ESDs of the CL by 98% compared to the ESD of the CS.

ESMF appeared to be less affected by the species loss scenarios. Out of the 25 combinations of land use types with scenarios, ESMF either increased or decreased only in 10 cases, otherwise, it remained the same (see Figure 5). The loss of rare species in BAU and EXT scenarios resulted in decreases of CL's ESMF by 4% in each scenario. However, unexpectedly, the ESMF of the IF increased by 3% and RL by 16% in the BAU and EXT scenarios. In the case of LUI and DEF scenarios, the ESMF of the AF decreased by 4% and the IF increased significantly by 7%. Unexpectedly, ESMF of the IF in RES scenario decreased by 3% relative to ESMF of the CS.

4. Discussion

4.1 Current distribution of trees and ES across land use types

We expected the IF and AF land use types to have higher diversity indices than the human modified land use types (EF, CL, and RL). However, this later group of land use types had the same or sometimes significantly higher tree diversity indices than the former group (Table 1). This might be explained by the planting of diverse tree species by the local community for multipurpose benefits (DeClerck et al. 2010; Burkhard et al. 2012).

Each land use type is characterized by typical ES (indicator ES, Figure 3, Table 2), but more ES were specifically associated with IF and AF. The protected native species in the IF– *J. procera, Afrocarpus falcatus, Olea europaea,* and many other species which were rare outside the forest – were a source of many specific ES. Local communities are highly dependent on IF for firewood and charcoal (Duguma and Hager 2010), farm implements, beehives, human medicine, toothbrushes, milk-flavoring, and heritage and culture services. Thanks to these services, the IF effectively serves as a financial 'safety net' during difficult times. Poor households sell charcoal, firewood, and timber to compensate food stock declines during the off-farm season (Duguma and Hager 2009). Farmers use specific trees for farm implements, particularly plow accessories (Gebregziabher et al. 2006). They usually prefer wood of *Sclerocarya gillettii, A. falcatus*, and *O. aequipetala* for plow making, because of the strength and durability of the wood. Direct human interventions favoring trees with specific ecosystem benefits could be an explanation for the strong association of other land use types with specific services. The EF was planted for the purpose of buffering the IF against encroachment and land degradation, and for timber production (Figure 3, Table 1), which is confirmed by the identified IES. A similar practice of tree planting around a protected area has been reported from Mount Elgon in Uganda (Sassen et al. 2013). The contribution of planted forests to ES supply could be improved either with the incorporation of indigenous trees in plantation practice (Tscharntke et al. 2012) or allowing natural regeneration of indigenous trees between and under the canopy of the exotic trees (Thijs et al. 2014). Most of the IES associated with agroforestry resulted from trees providing marketable products (such as *Carpobrotus edulis, Eucalyptus camaldulensis*, *Cupressus lusitanica, A. falcatus*, and *E. globulus*, edible fruits (*Mangifera indica*), and nitrogen-fixation (*Sesbania sesban, Acacia abyssinica*, and *Faidherbia albida)*. Among the economically important species, *C. edulis* (local name, chat) is a stimulant, and, as such, the provider of one of the most marketable non-timber forest products of the AF also planted around homesteads. *E. camaldulensis, E. globulus*, and *Cupressus lusitanica* offer significant sources of income from timber selling and are widely used in tropical tree plantations (Thijs et al. 2014). Farmers also plant nitrogen-fixing trees to improve soil nitrogen availability of their farmland, because tropical smallholder farmers lack financial resources to afford artificial fertilizer (Leakey 2014). Nitrogen-fixing trees can be a cheap alternative to commercial fertilizers (Munroe and Isaac 2014). Moreover, long-term experimental research revealed that legume trees increase the water-use efficiency and yield stability of agricultural crops in rain-fed agroforestry systems (Sileshi et al. 2011). Fruit trees such as *M. indica* enhance food availability at the household level and are sold on the market as well. The observed tree diversity in AFs is a deliberate choice of the farmers and a demonstration that the related diversification of products and services is more rewarding than monoculture practice, both from an economic and land protection point of view (Barrett et al. 2013). Trees in the open agricultural landscape are still present because of their desired properties that are useful on these land use types.

4.2 The effect of tree species loss and RES on ES

In a scenario analysis, we studied how species RES and different levels of nonrandom species loss affected the tree-related ES provided in different land use types. We found a positive relationship between species richness and ES supply (see Fig. S1 and S2), which corroborates the current consensus in the scientific community (Cardinale et al. 2012). We acknowledge that our methodology did not account for possible synergistic effects of species diversity on ES, which are reported to increase the provision of ES (Brittain et al. 2013). Our results can therefore be considered as a rather conservative estimation of ES provision.

The diversity–ES supply relationship was not affected by species loss or gain in the scenario analysis. The loss of rare species in BAU and EXT scenarios resulted in a low ESD in the agricultural landscapes CL and RL (Figure 5). This implies that the remaining common species could not compensate for the loss of ESD provided by the rare species. Rare species thus have distinct traits that considerably contribute to the ESD and that rare tree species are supporting the supply of ES in the agricultural land uses of the study area. Few studies have reported the contribution of rare species to ES provisioning. Mouillot et al. (2013) reported that rare species supported vulnerable functions in diverse ecosystems, because they often have distinct functional traits and perform unique ecological functions. The species loss caused by land conversion of AF and IF to CL (LUI and DEF scenarios respectively), led to a decline in ESD. This trend of biodiversity and the associated ES loss due to the forest and AF land conversion to CLs are also reported elsewhere (Tadesse et al. 2014; Sharma and Vetaas 2015). Finally, the recovery of rare tree species through RES increased ESD in IF, CL, and RL. This can be explained by the occurrence of less common species in these land use types, which is a typical characteristic of the tropical agricultural landscape (Herrera and García 2009).

ESMF was less affected by species loss. In the degradation scenarios (BAU and EXT), species loss seemed to be compensated by the remaining common tree species, as more or less the same level of ESMF is kept after the loss of rare species, in agreement with Walker et al. (1999). This result suggests that naturally occurring early successional tree species (*Acacia* spp., *Croton macrostachyus*) in the agricultural landscape might play a prominent and disproportional role in providing multiple services in human-modified landscapes (Manning et al. 2006; Fischer et al. 2010). The same pattern was observed in the land conversion scenarios (LUI and DEF). This seems counterintuitive but it is not surprising, as it shows that people prefer to use multifunctional trees on the CL. Individual trees that provide multiple services amply compensate for functions of the lost species (Metzger 2000). In practice, the local communities value and harness multifunctional species with a suite of ecosystem properties and useful services (e.g. nutritious, medicinal, firewood, and ornamental) (Burkhard et al. 2012) on human-modified landscapes.

5. Conclusions

In this study, we explored the effect of land use and land use change on the provision of ES in a mixed Afromontane landscape. Tree-related ES were clearly not randomly distributed over land use types, rather each land use type was characterized by distinct combinations of tree occurrence and corresponding tree-related ES. This highlights the conservation value of trees in forests, but also in open landscapes for the sustainable provision of ES. In different scenarios, the changes in ES provision following real-world processes of diversity loss and RES were assessed. The combination of two ES indices in this analysis gave us the possibility to reveal patterns that otherwise would not have been exposed. ESD takes into account the occurrence of the ES in the landscape, while ESMF only counts the number of ES that are maintained at a high level. We found a positive relationship between species richness and ES diversity. In land use types with low tree abundance and diversity, the local communities preferred multifunctional tree species that keep the number of ES high. Rare tree species play a considerable role in providing and sustaining specific ES that are not supported by the remaining common species after species loss. Overall, the findings of this study suggest that tree species loss including the loss of rare species has a considerable effect on ecosystem functioning and supply of ES. IFs and agroforestry patches play an important socioeconomic role in landscapes worldwide because of the unique ES they provide. Based on our findings, we recommend that tree species conservation programmes should not only focus on IF but should also target other land use types. We also advocate that both tree species diversity including the protection of rare tree species and the promotion of multifunctional keystone species should be included in future biodiversity conservation and RES programs to maintain and improve long-term ecosystem functions and services.

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Disclosure statement

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Highlights

- Land use intensification threatens trees and tree-related ecosystem services (ES) in landscapes worldwide
- We assessed the effect of tree species loss and restoration scenarios on ES provision in an Afromontane landscape
- Rare tree species provide unique ES
- Multifunctional tree species keep ES supply high in species-poor degraded landscapes
- Biodiversity conservation should focus on both multifunctional keystone and rare species to ensure long-term ES supply

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