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An ecological and socio-economical study of a locally endangered tree species, *Olea europaea* subsp. *cuspidata*, in a dry Afromontane forest

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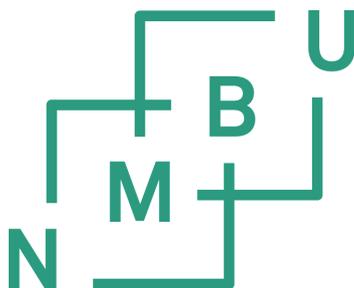
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Philosophiae Doctor (PhD) Thesis

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I dedicated this thesis to

my beloved late father, Ourge, Alemitu, Abebe, Albastros, Mule, Haymi

"If you cannot explain it simply, you do not understand it well enough"

(Albert Einstein)

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SUMMARY

Afromontane forests are found in the tropics and are often threatened because of land use changes. These forests have various types of multipurpose tree species that provide different services to the local communities. However, many of these species are being threatened because of overexploitation, and are therefore, locally endangered. Understanding the relationship between endangered tree species, and biotic, abiotic and human disturbance factors is important to understand their current and future distributions, at both local and larger scales, and to provide good plans for management and conservation. *Olea europaea* subsp. *cuspidata*, one of the multipurpose trees in dry Afromontane forests provides vital functions to the local communities. The species is under pressure from overexploitation and considered among the locally endangered tree species in Ethiopia.

This thesis consists of results from studies carried out in a dry Afromontane forest in Northern Ethiopia. The main aim of these studies was to examine which factors influence the performance of a multi-purpose and locally endangered tree species across different levels of organization, i.e. from individual reproductive success, different ontogenetic stages, and abundance on community level. We explored (1) how biotic, abiotic and disturbance factors influence the abundance and biomass of two key dry Afromontane forest species, (2) the population structure and if there are ontogenetic niche shifts in *O. europaea* in the forest, (3) how the disturbance and environmental factors are related with the reproductive success of *O. europaea*, (4) the extent of illegal logging of *O. europaea* in the study area, and what kind of actual benefits the species provide to the local communities. We used vegetation survey, soil samples and questionnaires to sample the data, and generalized linear models and, ordination analyses to analyse the data.

We showed that biotic, abiotic and disturbance factors explained over 40% of the variation in *O. europaea* abundance and that there was a positive relationship between two endangered

species, *O. europaea* and *Juniperus procera* and woody species richness, but also an effect of human disturbance. Ontogenetic niche shifts were observed in *O. europaea,* suggesting that seedlings, saplings, and adults are differently related to woody species richness, soil depth, slope and logging. We also found a negative relationship between the reproductive success of *O. europaea* and human disturbance. Even if the forest is protected by guards, there is still illegal logging taking place.

With these studies, we concluded that because of the positive relationship between the two tree species and woody species richness, we recommend the forest administrators should consider conserving woody species in general to promote *O. europaea* and *Juniperus procera* abundance in degraded areas. For protecting the few *O. europaea* seedlings in the forest, special attention should be given to protect them from browsing. Moreover, human disturbance is the main factor influencing reproductive success and a reason for illegal logging in the forest. Therefore, we would suggest that allowing the local community to harvest dead wood from the forest might reduce the illegal logging. Finally, we would also suggest establishing permanent plots for monitoring the extent of illegal logging of *O. europaea* in the forest.

LIST OF PAPERS

Paper I

Wegasie, M.O., Klanderud, K., Eldegard, K, Tewolde-Berhan, S., Giday, K., Totland, Ø. (2018). Locally Endangered Tree Species in a Dry Montane Forest are Enhanced by High Woody Species Richness but Affected by Human Disturbance. *Journal of Arid Environments*. https://doi.org/10.1016/j.jaridenv.2018.08.001

Paper II

Wegasie, M.O., Klanderud, K., Totland, Ø., Eldegard, K. Ontogenetic niche shifts of a locally endangered tree species (*Olea europaea* subsp. *cuspidata*): implications for conservation. Submitted manuscript

Paper III

Wegasie, M.O., Eldegard, K., Tewolde-Berhan, S., Totland, Ø., Klanderud, K. The relationship between reproductive success of a locally endangered tree species, *Olea europaea* subsp. *cuspidata* and human disturbance in an isolated Afromontane forest in northern Ethiopia. Manuscript

Paper IV

Wegasie, M.O, Hofstad, O., Klanderud, K., Eldegard, K., Tewolde-Berhan., Sarah (2018). Illegal Harvesting of Locally Endangered *Olea europaea* Subsp. *cuspidata* (Wall. ex G. Don) Cif. and Its Causes in Hugumburda Forest, Northern Ethiopia. *Forests* **2018**, *9*(8), 498; doi: 10.3390/f90804

SYNOPSIS

1. INTRODUCTION

1.1. Multipurpose tree species in the tropics

Multipurpose tree species are woody perennials that provide more than one service to the human community (Wood and Burley, 1991, Price et al., 2011). The services could be provisioning, regulating, supporting and cultural (Foroughbakhch et al., 2009). In the tropics, there are many multipurpose tree species, for example, *Moringa oleifera*, *Jatropha curcas, Ziziphus spina-christ,* and several others known for their timber and non-timber benefits (Olson and Fahey, 2011, Kumar et al., 2011). However, many of them are being threatened because of overexploitation (Sinébou et al., 2016), and are therefore, categorized as locally endangered plant species (Herrero-Jáuregui et al., 2013). For instance, species like *Rheum austral, Erythrina abyssinica, Hagenia abyssinica, Juniperus procera, Olea europaea* subsp. *cuspidata* are among locally endangered, multipurpose plant species (Feyissa et al., 2005, CBD, 2009, Kirika et al., 2015, Pandith et al., 2018). The reason could be that the trees are often the only resources for plant material, particularly for firewood for the poor communities, and fodder for their livestock (Arnold, 1987, Dawson et al., 2014). However, there are unresolved conflicts between the use and management of these species (Herrero-Jáuregui et al., 2009, Herrero-Jáuregui et al., 2013). For instance, according to a study conducted by Masozera and Alavalapati (2004), the local people's dependency on the forest for fuelwood and for generating income created conflicts between biodiversity conservation and community needs, in a pine plantation managed as a buffer and habitat for wildlife in Rwanda. Therefore, for effective conservation of multipurpose tree species, there should be a balance between conservation and their use (Adams et al., 2004).

1.2. Afromontane forests and the role of environmental and human disturbance factors

Afromontane forests are found in the tropics, and are often threatened ecosystems because of land use changes, natural and human disturbances (DeFries et al., 2005, Tesfaye et al., 2010), and they are characterized by their discontinuous vegetation assemblages on isolated mountains called "forest island" (Meadows and Linder, 1993). They are typically surrounded by agricultural fields in the lowlands, and often have high species diversity (White, 1981, 1983). The distribution of Afromontane forests stretches from the mountainous part of Africa to the southern Arabian Peninsula, and, in a fragmented form, covers West and East African highlands, Arabian highlands, and parts of the Cape Peninsula (White, 1983). The Eastern Afromontane forests cover about 1,017,806 square kilometres, in Eastern Arc Mountains in Kenya and Tanzania, Southern and Albertine Rift, and the Ethiopian Highlands. These forests contain approximately 7,600 plant species, among them, 2,350 are endemic (Profile, 2012).

Afromontane forests are under high pressure due to anthropogenic factors, such as land use change and logging (Alston and Richardson, 2006). Therefore, these human disturbance activities are affecting the population structure of the plants, which may result in biodiversity loss (Sala et al., 2000). Moreover, human disturbances, such as tracks made by people and their livestock indicate accessibility of the forest, and can also increase accessibility and, thus, harvesting of trees (Sinébou et al., 2016). High harvesting of branches and leaves may affect the tree populations, and the flowering and, thus, the reproduction of the species in particular (Oumorou et al., 2010). Understanding tree species responses to environmental factors and to human disturbance is important for developing sustainable management and conservation plans (Walthert and Meier, 2017).

In Ethiopia, Afromontane forests previously constituted 35-40% of the total vegetation. However, due to human disturbance such as agriculture expansion into the forest fringe, over-exploitation and land use change, only few forest fragments remain (DeBusk Jr, 1998, Wakjira, 2006). They are distributed in the central, northern, eastern and southern parts of the country (see review in Tura et al., 2017).

1.3.   Use and distribution of *Olea europaea* subsp. *cuspidata*

Olea europaea subsp. *cuspidata* is one of the subspecies in the Olive (Oleaceae) family. The tree has a wide distribution range from Southern to Eastern Africa, and in some parts of the Arabia, India, and China. The tree resists both drought and frost (Bekele-Tesemma and Tengnäs, 2007). It is a characteristic tree species, together with *Juniperus procera,* in dry Afromontane forests, and widely used for timber production (Aerts et al., 2006, Walthert and Meier, 2017). The leaves can be used as medicine (Long et al., 2010), and the roots for traditional smoke bath (Ourge et al., 2018).

Even though *Olea europaea* subsp. *cuspidata* is a locally endangered, multipurpose tree species in its native range, in places like Australia and Hawaii, it is categorized as a problematic species (Cuneo and Leishman, 2006, Besnard et al., 2007). There is a dilemma being both an endangered and an invasive species (Marchetti and Engstrom, 2016), as some species can be problematic out of their native range, but useful in their natural place. According to the enemy release hypothesis, this may be because plants have less enemies or competitors when they are introduced to a new area, which enable them to dominate over native species (Keane and Crawley, 2002).

Olea europaea subsp. *cuspidata* (hereafter *O. europaea*) is indigenous to Ethiopia, with a distribution from 1250 to 3100 m a.s.l. in the dry Afromontane forests, e.g. Hugumburda Afromontane forest (Fig. 1a). The adult trees normally grow up to 15 m high

(Fig. 1b), but they can reach 25 m (Friis, 1992). It is pollinated by wind, and birds disperse the fruits. The flowers are cream colour (see Fig. 1c) and are 6-10 mm long with both male and female organs. The fleshy fruit has a diameter of 10 x 8 mm with an oval shape (see Fig. 1d). The immature fruit is green, and brownish when it has ripened (Abiyu et al., 2016). The population of *O. europaea* is decline because of overexploitation and it is recognized as a locally endangered species in Ethiopia (CBD, 2009).

Although many studies have been carried out on the plant species diversity of Afromontane forests, little attention has been given to how the response of threatened multipurpose tree species in general, or, *O. europaea* in particular, are related to biotic, abiotic and human disturbance factors. Biotic factors may determine plant abundances at local and larger scales through species interactions, such as facilitation or competition (Kimmins, 2009, Maestre et al., 2010). In addition, abiotic factors, such as topography and soil also play a significant role in determining plant species abundance (Williams-Linera and Lorea, 2009), and human disturbance is a reason for land use change in densely populated areas (Profile, 2012).

1.4. Study aims and questions

The aim of this study was to explore the performance of *O. europaea* across different levels of organization, from population to community level, and how these relate to the environmental conditions and to the human disturbances in Hugumburda forest in Ethiopia. The four major questions addressed in this study are: (1) how do the abundances and biomass of two endangered tree species, *O. europaea* and *Juniperus procera*, relate to environmental and human disturbance factors (**Paper I**)? (2) do the different life stages (seedlings, saplings, adults) of *O. europaea* respond differently to biotic, abiotic and human disturbance factors (**Paper II**)? (3) how does the reproductive success of *O. europaea* relate to environmental conditions and human disturbance (**Paper III**)? (4) what are the benefits from *O. europaea* to

the local community, and what is the extent of the illegal harvest of *O. europaea* wood in the forest (**Paper IV**)?

2. MATERIAL AND METHODS

2.1. Study area

Hugumburda is an isolated Afromontane forest located at 12^0 22'– 12^0 42' N, 39^0 28'–39^0 40' E in Tigray region, North Ethiopia. The landscape of the forest is mainly rugged and mountainous, with an elevation range of 1860–2700 m. a.s.l. The soil depth is shallow and dominated by leptosols and regosols soil types (Aynekulu, 2011). The average daily temperature range is 14.6 –22.4°C, with annual minimum of 8.8°C in October and a maximum of 34.3 °C in June. The annual rainfall range is 705–986 mm (Woldemichael et al., 2010).

Hugumburda is a secondary forest (Aynekulu, 2011) and has a high diversity of trees, bushes, lianas, and herbs and includes some residential areas and agricultural fields on the borders of the forest. According to Woldemichael et al. (2010)'s importance value index calculation, the dominant tree species in the forest are *Juniperus procera, Olea europaea* subsp. *cuspidata* (see Fig. 1b)*, Nuxia congesta, Cassipourea mallosana,* and *Olinia rochetiana*. The forest is surrounded by 26,889 households and among them, 5496 households live inside the forest (Kidane et al., 2018). According to the local community, in the 1950s there was commercial timber production undertaken by an Italy company in the forest. In 1993, the forest was officially recognized as one of the National Forest Priority Areas in Ethiopia (Woldemichael et al., 2010). In Ethiopia, 58 National Forest Priority Areas (NFPA's), which cover 3.6 million hectares have been identified and delineated to conserve biodiversity loss and promote educational visits and research activities (MEFCC, 2017).

Figure 1 a) landscape view of Hugumburda forest, northern Ethiopia; b) *O. europaea* tree in Hugumburda forest; c) *O. europaea* flowers on a tree; d) *O. europaea* fruits (mature: brown and not mature mixed: green) harvested for fruit counting. Photos: Wegasie, M.O

2.2. Field data collection

2.2.1. Vegetation survey

Seventy 20 × 20 m plots were positioned on forested slopes at elevations of 2233-2503 m.a.s.l. in 2015. The plots were distributed about 100 m apart along parallel transects placed perpendicular to three local terrain ridges, each transect running from the top to the bottom of the ridge (Figure 2). The distance between neighboring transects was ca. 150 m.
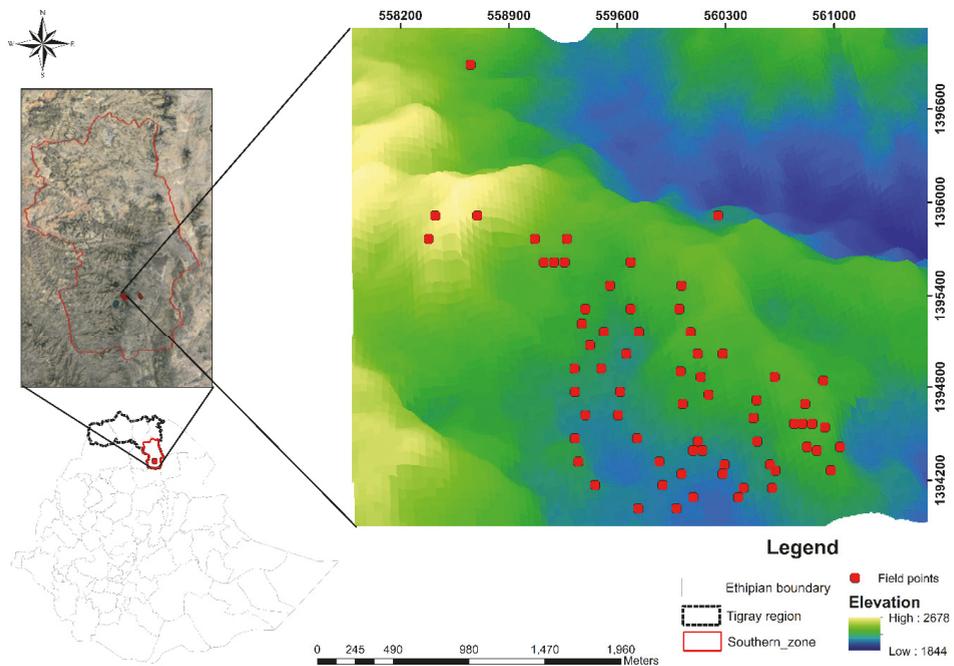
Figure 2. Locations of the study plots in Hugumburda forest, Northern Ethiopia

In each 20 × 20 m main plot, we identified, counted and recorded all adult trees and shrubs to species level. We measured stem diameter at breast height (DBH) of individual trees, basal diameter (BH) for each shrub, and the heights of both shrubs and trees. The abundance and species identities of saplings were recorded in one 5 × 5 m sub-plot, placed in the center of each main plot. The number and identities of seedlings was recorded in five 1 × 1 m small plots, one placed in the center of each main plot and four at the corners of each 5 × 5 m sub-plot (see Fig. 3). We also visually determined the percent cover of herbaceous species within each small plot. We used plant height and diameter at breast height to classify each woody individual into adult, sapling or seedling.

2.2.2. Environmental and Human disturbance factors

We sampled environmental and disturbance variables in the same 20 × 20 m plots as we sampled the vegetation data. To quantify human disturbance, we used a measuring tape to estimate the total length (m) of tracks in each main plot, using these tracks as one indicator of disturbance of both humans and domestic animals. We also counted the number of *O. europaea* stumps and used that as an indicator of logging.

To study the relationship between *O. europaea* trees and abiotic environmental variables, data on slope and elevation, and soil samples were taken. Slope and elevation were measured using clinometer and a handheld GPS, respectively. Two separate soil samples were collected for soil moisture content (by soil core samplers) and chemical analyses (soil moisture, soil pH, electrical conductivity, and soil organic matter). Soil depth was measured in the field by digging a pit at the center of the main plot down to the bedrock.
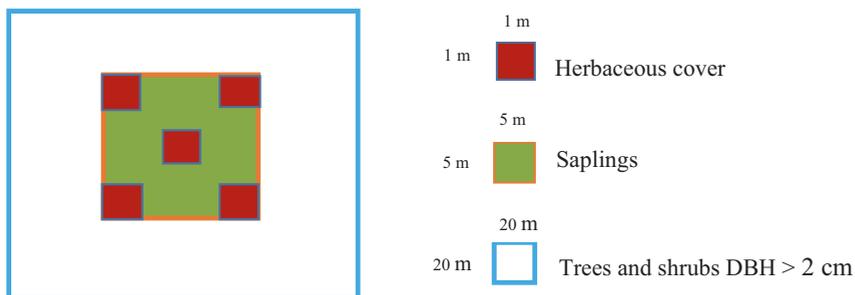
Figure 3. Sample plot design used during the fieldwork in Hugumburda forest

For the reproductive parameters (**Paper III),** we selected one *O. europaea* tree in each 20 × 20 m main plot. On each of the selected *O. europaea* trees, ten branches were chosen randomly and marked at 25 cm from the tip to the middle. The sampled trees were monitored three times until fruit maturation. First, the number of flowers and leaves on the marked branches were counted during the flowering period (June 2015). All marked branches were revisited for a second time (September 2015) to count the number of pre-mature fruits. We counted premature fruits to avoid data loss during the fruit maturation period, as ripening fruits are commonly eaten by birds (Abiyu et al., 2016). We counted mature fruits in October 2015.

For **Paper IV**, we conducted a socio-economic survey in three villages (Kukufto, Hashenge, and Tahtay Haya) to assess how human needs and activities relate to the harvesting of *O. europaea* in the nature reserve. Representatives of 162 households, that is 54 respondents from each village, were interviewed. Systematic stratified sampling was used to select households, with the aim of including both genders and different economic statuses, age classes, and educational backgrounds. A semi-structured questionnaire (Appendix 1) was administered to get information about the different uses of *O. europaea* wood to local communities.

2.3. Derived variables

Woody species richness was defined as the total number of tree and shrub species observed in a sample plot, and abundance as the number of individuals counted in each main plot.

In **Paper I, II & IV**, aboveground biomass for all trees was estimated using an allometric equation developed for tropical forest (Chave et al., 2014).

In **Paper II**, simulated values were determined by random relocations of the sampled seedling, sapling and adult trees from all sample plots using the reshape2 package in R. Moreover**, Paper II** provides a novel approach of testing observed data with simulated data that could advance the studies of ontogenetic niche shifts in plant populations.

In **Paper IV**, aboveground *O. europaea* biomass was estimated using the allometric equation developed by Parent (2000) of *O. europaea* trees in Ethiopia, and *O. europaea* wood annual harvesting rate was determined by calculating the aboveground biomass of all *O.europaea* tree stumps diameter with their corresponding time since cut (i.e. stump age) and dividing by 400 m^2 (main plot size).

2.4. Statistical analysis

Different types of generalized linear models were used to examine patterns and relationships between the abundance, biomass, and reproductive success of *O. europaea,* and environmental and disturbance factors in the forest.

Generalized linear models (GLM) and Nonmetric Multidimensional Scaling (NMDS) analyses were used to explore and determine the relationship between the abundance and biomass of two dominant tree species, *O. europaea* and *Juniperus procera* and biotic, abiotic and human disturbance (**Paper I**), and the association between the seedlings, saplings, and adults of *O. europaea* and as well as environmental and disturbance factors (**Paper II**).

Logistic regression analyses were used to determine the likelihood of finding the different *O. europaea* life stages in the plots. The interaction term between the life stages and biotic, abiotic and disturbance factors was used to assess whether the influence of these factors varied among the life stages and thus reveal ontogenetic niche shifts (**Paper II).** We used similar logistic regressions analyses to estimate the likelihood of *O. europaea* being harvested from Hugumburda Forest (**Paper IV**). Hurdle and generalized mixed effect models (GLMM) were used to explore the relationship between the reproductive success of *O. europaea* and tree attributes as well as abiotic and disturbance factors (**Paper III**). In **Paper IV**, linear and generalized linear models were used to assess the relationship between *O. europaea* harvesting rate and distance to the forest, and number of *O. europaea* stumps and distance to the forest, respectively.

3. RESULT AND DISCUSSION

3.1. Thesis overview

Taken together, in **Paper I,** we found that *O. europaea* abundance was positively related with the abundance of another dominant tree species, *Juniperus procera,* and woody species richness. However, human disturbance factors such as logging and track length influenced *O. europaea* abundance and biomass (**Paper I**). In **Paper II**, three *O. europaea* life stages responded differently to woody species richness, soil depth, slope, and logging, suggesting ontogenetic niche shifts in *O. europaea*. In **Paper III**, we found that the reproductive success of *O. europaea* was negatively related to human disturbance factors (i.e. tracks of humans and their livestock in the forest). In **Paper IV**, we showed that *O. europaea* has multiple benefits to the local community. Moreover, we found that there is illegal logging of *O. europaea*, with 430 kg ha^{-1} being harvested per year despite the fact that the forest is protected.

3.2. The relationship between *O. europaea* and biotic, abiotic and disturbance factors

The results reported in **Paper I** indicated that there is a positive relationship between the abundance and biomass of *J. procera* and *O*. europaea (**Paper I**, Fig. 1a & b), and with woody species richness (**Paper I**, Fig. 2). The positive relationship between the two multi-purpose tree species and woody species richness may be due to facilitation which can promote the conservation of tree species (Gómez-Aparicio, 2009). For instance, Maestre et al. (2012) showed that woody species richness can positively influence the abiotic environment by increasing soil fertility through facilitating carbon and nitrogen cycling in dry forest ecosystems. An alternative explanation for the positive relationship could be niche partitioning between abundant tree species in arid areas, suggesting that *J. procera* and *O. europaea* coexist because they have different resource requirements (Hubbell, 1980, Fetene and Feleke, 2001, Peterson et al., 2013).

We also found a positive relationship between the abundance and biomass of the two characteristic tree species and abiotic factors, such as slope and elevation (**Paper I**, Fig. 2; Fig. 4), suggesting that these factors may play a significant role in the distribution of these tree species in dry Afromontane forests (Mehnatkesh et al., 2013, Måren et al., 2015). The reason for the higher abundance of *O. europaea* and *Juniperus procera* at higher elevations could be that these species are able to grow on rocky ground, and at steep slopes of the forest, because of their ability of withstanding the dry conditions (Bekele, 2000, Wubet et al., 2003, Aerts et al., 2006). We also found that the biomass and the abundance of *O. europaea*, and the number of cut *O. europaea* stumps in the forest were positively correlated (**Paper I**, Fig. 2; Fig. 3). This suggests that the local community undertake selective logging in dense stands

of *O. europaea* (as also seen in **Paper IV**). Therefore, special attention should be given to *O. europaea* and *Juniperus procera* dominated areas of the forest.

3.3.   Population structure and ontogenetic niche shifts in *O. europaea*

Studying the population structure and ontogenetic niche shifts of endangered tree species is important for choosing optimal conservation strategies to manage the plant species. We found lower densities of seedlings than saplings and adults (**Paper II**, Fig. 1; Fig. 2), and it seems like there is lower regeneration of *O. europaea* in the Hugumburda forest compared with other Afromontane forests in the region. The reason for this low regeneration could be excessive browsing of seedlings by livestock (Aerts et al., 2007).

We also tested if there are ontogenetic niche shifts in *O. europaea*. We did this by testing for interactions between three different life stages in terms of how they relate to different biotic, abiotic and human disturbance factors (**Paper II**). The results showed that the seedlings, saplings and adults are related differently to woody species richness, soil depth, slope, and logging, suggesting ontogenetic niche shifts (**Paper II**, Fig. 4; Table 2).

There was higher probability of *O. europaea* seedlings occurring in area with deeper soils. This is likely because deeper soil holds more moisture than shallow soil, and seedlings require moisture to establish (Bekele, 2005). However, the probability of finding *O. europaea* saplings decreased with soil depth. The reason could be that both saplings and adults were more abundant at higher elevations, where the soil is also shallower (as seen in **Paper I**).

The probability of finding saplings and adults of *O. europaea* increased with woody species richness (**Paper II**, Fig. 4) (Maestre et al., 2012). We speculated that this could be

due to facilitation since *O. europaea* seedlings can easily grow under the shade of woody species, e.g. *Euclea racemosa* as a nurse plant (Aerts et al., 2007).

The probability of finding *O. europaea* seedlings, saplings and adults responded differently to logging. The probability of finding seedlings and adults increased with logging, whereas saplings decreased. This suggests that logging is higher in areas where adult trees dominate, and that logging may favour seedlings because it might reduce competition from older trees. Quantifying the logging and harvesting rate, and understanding why and where illegal harvesting is occurring, was a topic we examined in detail in **Paper IV**.

3.4.   The relationship between reproductive success of *O. europaea* and human disturbance

In **Paper III**, we found that the likelihood of *O. europaea* flowers occurrence was higher with wider canopies, and lower with increasing soil depth (**Paper III**, Fig. 1; Table 1). A tree with wider canopy may have higher biomass, and thus more resources are available for flowering (Sanni et al., 2018).

The likelihood of *O. europaea* flowers and premature fruits resulting in mature fruits was negatively related with human disturbance (track length) in the forest (**Paper III**, Fig. 2; Fig 3). The reason could be that tracks made by people and animals could create more gaps, which could hinder pollination (Sayago et al., 2018). In addition, human disturbance effects, by lowering pollination attraction and increasing inbreeding, on reproductive success has been observed on fruit production in *Mediterranean orchids* in Italy (Pellegrino and Bellusci, 2014). An alternative explanation for the low fruit production may be due to a fly feeding on premature *O. europaea* fruits (Mkize et al., 2008), which could lead to abscission of fruits (Stephenson, 1981).

Reproductive success is a chained process. If one stage get negatively affected, it would be problematic for the next. The low availability of fruits could be a bottleneck for seedling recruitment because of less availability of seeds in the soil seed bank (Sinébou et al., 2016). This might be one reason for the low seedling density in the *O. europaea* population, as presented in **Paper II**.

3.5. The extent of illegal harvesting of *O. europaea* and its causes

Paper IV shows that *O. europaea* trees are used for different purposes, including farm implements, fuelwood, and fumigation. Because of that, ca. 2,000–5,000 tons was logged in Hugumburda forest during the study year 2016. *Olea europaea* wood is used for firewood or charcoal because it burns slowly and has a high calorific value with little smoke (Wubet et al., 2003, Gebreslassie et al., 2014). We observed that small trees were cut more frequently than the large ones, likely because small trees are easier to cut and carry with the tools available (Leach and Mearns, 2013).

We found a positive relationship between the harvesting rate and elevation (**Paper IV**, Fig.3; Table 2), and there was humped back relationship between the number of stumps and distance from the nearest village (**Paper IV**, Fig.4; Table 3). The positive relationship between *O. europaea* harvesting rate and elevation suggests that because of the high abundance of *O. europaea* at higher elevation, local people do frequent logging there. In addition, the reason for the humped back relationship between the number of stumps and distance from the nearest village could be because of the very nearest part of the forest might be already logged, and as a result, people are cutting *O. europaea* tree at intermediate distances (ca. 1.5–2.5 km) from the village.

We also found that there is a higher demand for *O. europaea* wood in the villages around Hugumburda forest than in the bigger city Mekelle. The reason could be that *O. europaea*

wood sold in the big city probably comes from many sources, and the competition among suppliers may keep the prices for the wood relatively low. The higher demand of *O. europaea* by the local community could increase the probability of illegal harvesting in forests. Although there are rules and regulations that prohibit the harvesting of *O. europaea* in Hugumburda Forest, this is still a problem.

4. CONCLUDING REMARKS AND FUTURE PERSPECTIVES

Tree species in Afromontane forests are susceptible to anthropogenic factors due to land use change and over-exploitation (Alston and Richardson, 2006). Therefore, understanding the relationship between endangered tree species and biotic, and abiotic environmental factors, and human disturbance is urgent to develop sound management strategies (Kimmins, 2009, Maestre et al., 2010).

Paper I shows that conserving woody species richness may promote the conservation of the two multi-purpose tree species, *Olea europaea* and *Juniperus procera* as well as the entire forest. In addition, the positive relationship between *O. europaea* and *J. procera,* and with other woody species in the forest suggests even if *O.* europaea is problematic in other areas, this is not the case within its native range in Hugumburda forest. The high number of cut stumps show that selective illegal logging is common in *O. europaea*-dominated areas in the forest (**Paper IV).** Human disturbance is also negatively related to reproductive success (**Paper III)** and likely decline population density over the long term (**Paper II**). Controlling human disturbance could help conserving the forest resources at local and national scale, and we recommend different tools to conserve endangered tree species in general and *O. europaea* in particular. First, the management plan for conserving endangered tree species in dry montane forests should include conserving woody species in general, as this, in turn, can promote the abundance of locally endangered tree species. Second, low regeneration rates

and drought stress appear to be the main constraints for *O. europaea* seedlings to establish. Thus, special attention should be given to protect seedlings from browsing. Third, illegal harvesting of *O. europaea* wood is being done because people need fuelwood, fumigation and farm implements. The local people are poor and do not have other alternative sources. Therefore, allowing the local community to harvest dead wood from the forest might reduce the illegal logging. Finally, we recommend the establishment of permanent sample plots in the forest to monitor the increment of *O. europaea* as well as other tree species to control the intensity of the illegal logging in the forest.

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APPENDIX

Questionnaire format used for interviewing farmers living around Hugumburda forest

❖ NOTE: *Olea* is denoted *Olea europaea* supsp. *cuspidata*

Date of Interview:__ _____
Name of interviewer: _____ _____
Name of interviewee: ____
Age: _____   sex: _____   Marital status: ___   **Position in the household: _____   Level of education: _____**
Family size: _____   No of children: _____
Interview number: _____   work:_____
Address: _____
Specific site name: _____
Economic status: ☐ **Poor**   ☐ **Middle**   ☐ **Rich**

Part I. <u>**Preliminary questions**</u>

A. Do you know Hugumbirda forest?

☐ Yes ☐ No

B. Are you benefited from the forest?

☐ Yes ☐ No

C. **Would you mention the benefits that you getting from the forest?**

D. Please quantify the amount of benefits that you get from the forest? (How much would be the quantity of wood that you get from the forest?)

E. Do you know the species *Olea* tree?

☐ Yes ☐ No

E. What kind of benefits do you get from *Olea* tree?

_____

F. Have you an access to the forest to get some *Olea* product?

☐ Yes ☐ No

G. Is *Olea* tree abundance increase or decrease in the forest?

☐ Increase ☐ Decrease

H. Do you know the reason why increased or decreased? (please describe by comparing the past and current) _____

Part II. <u>Questions about fuelwood</u>

1. **What type of energy sources do you have?**

   _____

2. **Which one is commonly used and why?**

   _____

3. **Do you use fuelwood for cooking?**

   _____ _____

4. **Would you mention the name of tree species used for fuelwood?**

   _____

5. **Which plant species is highly demanded for fuelwood?**

   _____

6. **What is the reason for the above question?**

   _____

7. **Do you use *Olea* tree as a fuel wood?**

   _____

8. **No. of years using Olea for fuel wood_____**

9. **How much Olea wood do you use for cooking once? (in quantity)**

   _____

10. **From where do you get *Olea* wood?**

    _____

    Part III. <u>Question about fumigation</u>

1. **No. of years using *Olea* for fumigation: _____**

2. **What is the purpose of being fumigated?**

   _____

3. **Do you use different plant species for fumigation?**

   _____

4. **Please list down the name of the species used for fumigation?**

   _____

5. **Which species are used for what purpose?**

   _____

6. **Do you use *Olea* for fumigating your home?**

   _____ _____

7. **Do you mix *Olea* with other species for fumigation purpose?**

   _____

8. **If yes, how much would be the quantity of *Olea* in the mixture?**

   _____

9. **Where do you get the *Olea* wood for fumigation?**

   [ ] **From home garden**   [ ] **from hugumbirda the forest**

   from the local market [ ]   [ ] **from Gebriel church**

   If you know another means to get Olea, please

   specify_____

10. **If your answer for the ninth question is from the market, how much does it cost you to buy a bundle of *Olea* wood for fumigation purpose (in birr)?**

    _____

11. In the local market, in what way *Olea* is being sold?

☐   **Bundle of Olea wood**   ☐   **in kg**

12. How much weight would be the bundle of *Olea* in Kg?

_____

13. Which gender is frequently fumigated with *Olea* smoke?

☐   **Female**   ☐   **male**

14. Why male or female is frequently fumigated with *Olea* smoke?

_____

15. How frequent you use *Olea* wood for fumigating your home?

_____

16. How much time will you spend by being fumigated once?

_____ _____

17. For fumigating once, how much *Olea* wood do you use?

_____

16. How could you prepare *Olea* woods for fumigation purpose?

_____ _____

18. In which season fumigation with *Olea* is highly demanded?

_____

19. Why is that season? (Based on question 19)

_____

Part IV. Question for farming equipment

1. **When did you start farming?**

   _____

2. **What are the major type of farm implements made of woods?**

   _____

3. **Do you use *Olea* tree for farming implements?**

   [ ] Yes   [ ] No

4. **No. of years in using *Olea* for farm implements: _____ ____**

5. **Would you mention the type of farming implements that can be made from *Olea* wood?**

   _____

6. **What is the frequency of replacement of your *Olea* made farm implements?**

   _____ _____

7. **Where do you get the *Olea* wood for making farming implements?**

   _____

8. **Why do you prefer *Olea* than other species?**

   _____ _____

9. **Is there another species used for making farming implements?**

   _____

10. **Please mention the name of other species used for making farming implements?**

    _____

Part V. Questions for livestock forage

1. **Do you have livestock?**

    _____

2. **How many cattle do you have?**

    _____ _____

3. **How many sheep do you have?**

    _____ _____

4. **How many goats do you have and what do you feed them?**

    _____

5. **What do you feed your cattle?**

    _____

6. **Do you get some fodder for your livestock from the Hugumbirda forest?**

    [ ]   Yes   [ ]   No

7. **Do you use Olea tree as a fodder for your cattle?**

    [ ]   Yes   [ ]   No

8. **If your answer is yes, would you tell us the place where you get Olea?**

    _____

9. **Which part of the Olea tree is highly preferred for fodder?**

    _____

10. **In which season, *Olea* fodder is highly demanded?**

    _____

11. **Why is that season? (based on question 15)**

    _____

Part VI. Questions about _Olea_ toothbrush

1. **No. of years in using Olea toothbrush: _____**

2. **Which kind of toothbrush do you choose?**

   ☐ **Natural**   ☐ **Fabricated**

3. **If your answer for the first question is natural, then why you choose natural toothbrush than the fabricated one?**

   _____

4. **Do you use _Olea_ tree as a toothbrush?**

   ☐ **Yes**   ☐ **No**

5. **Which thickness of _Olea_ tree is more preferred one?**

   _____

6. **Where do you get _Olea_ toothbrush?**

   _____

   ____

7. **What is your favorite type of natural toothbrush?**

   ☐ **_Olea_**   ☐ **Other species**

   - **If your answer for the above question is other species, please specify your favorite type of toothbrush species_____**

8. **Have you an experience of buying _Olea_ toothbrush?**

   ☐ **Yes**   ☐ **No**

9. How much it costs for one single stick of *Olea* toothbrush?

_____ _____

10. Do you know any supplier that supplies *Olea* toothbrush?

☐ Yes   ☐ No

11. If your answer is yes for the above question, do you know from where the supplier get *Olea* toothbrush?

_____

_____

12. Have you planted *Olea* tree in your garden?

☐ Yes   ☐ No

Part VII. Preference ranking

13. Which part of *Olea* tree is frequently used for fumigation?

No	Olea tree parts	Respondents rank										Rank	Remark
		R1	R2	R3	R4	R5	R6	R7	R8	R9	R10		
	bark												
	leaves												
	braches												
	stem												

No	Olea tree parts											Rank	Remark
	root												

14. Which part of *Olea* tree is frequently used for fuel?

No	Olea tree parts	Respondents rank										Rank	Remark
		R1	R2	R3	R4	R5	R6	R7	R8	R9	R10		
	bark												
	leaves												
	braches												
	stem												
	root												

15. <u>Which part of *Olea* tree part is preferred for farm implements?</u>

No	Olea tree parts	Respondents rank										Rank	Remark
		R1	R2	R3	R4	R5	R6	R7	R8	R9	R10		
	Sap wood												
	Heart wood												
	braches												
	stem												
	root												

Paper I
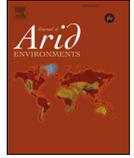
Locally endangered tree species in a dry montane forest are enhanced by high woody species richness but affected by human disturbance

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ARTICLE INFO

ABSTRACT

Understanding the relationship between biotic, abiotic and disturbance factors in dry degraded forests is crucial for effective conservation of endangered plant species. We studied the relationship between two locally endangered tree species, *Olea europaea* subsp. *cuspidata* and *Juniperus procera*, and environmental conditions in the Hugumburda dry Afromontane forest in Northern Ethiopia. We surveyed species richness of woody plants, herbaceous plant cover, soil and human disturbance factors from 70 plots (20 m × 20 m). The abundance of both species was positively correlated with each other, and with woody species richness and elevation. Moreover, the biomass of both species correlated positively with total tree biomass and number of *O. europaea* cut stumps. The positive relationship between *O. europaea* trees and cut stumps suggests that illegal selective logging is taking place in *O. europaea*-dominated areas. Based on the observed relationships we predict that conserving woody species may result in an increase in the abundance of both *O. europaea* and *J. procera* in the forest.

1. Introduction

In the tropics, human-induced natural forest degradation has become a serious problem (Lamb et al., 2005; Parrotta et al., 1997; Watson et al., 2014), and threatens the abundance of multi-purpose plant species. The cover of the world's natural forests is decreasing annually by 0.5% (Brockerhoff et al., 2013), which is reducing the benefits received from these areas by way of ecological services (Isbell et al., 2017; Teketay, 2001). To protect degraded forest with the aims of conserving endangered plant species in situ and maintaining ecological services, a program of establishing National Forest Priority Areas has been launched in different biodiversity hot-spots, including natural forest (M. Bekele and Berhanu, 2001; Margules et al., 2002; Veríssimo et al., 2002; Watson et al., 2014). But simply establishing protected areas may not be sufficient to conserve endangered plant species (Schemske et al., 1994). Therefore, studying the relationship between biotic and abiotic factors in protected areas may contribute positively to the goal of restoring degraded areas (Callaway and Walker, 1997; Holl et al., 2000; Michalet et al., 2006).

One of the determinants of plant species coexistence, and a key factor controlling plant species composition and distribution, is the relationship between biotic factors, such as richness and abundance of plant species, and the abiotic components of an ecosystem (Kimmins, 2009; Maestre et al., 2010; Shirima et al., 2015). For biotic factors, plant-plant interactions can involve either facilitation or competition (Leigh, 1999; Maestre et al., 2005). Facilitation, in which the presence of one species positively influences the abundance of another, is common in arid environments. It is relevant when conserving endangered tree species because such species may depend on interactions with others for their persistence. For instance, pioneer plants may facilitate the growth and abundance of the later plant species by ameliorating site conditions (Duncan and Chapman, 2003; Gómez-aparicio et al., 2004). In addition to biotic factors, abiotic factors such as elevation (used as a proxy for temperature), slope and soil parameters, together with natural and human-induced disturbances, also determine the plant-species composition and diversity in a forest (Williams-Linera and Lorea, 2009). For instance, in dry Afromontane forests, late successional plants are more abundant at higher elevation than low elevations (Aerts et al., 2011).

The Hugumburda forest is one of the 58 National Forest Priority Areas in Ethiopia, established to conserve biodiversity in the face of severe forest degradation in recent decades (Woldemichael et al.,

2010). Dry montane forests have relatively low woody species richness, and this particular forest area is dominated by the late successional plant species, *Olea europaea* subsp. *cuspidata* (here after *O. europaea*) and *Juniperus procera* (hereafter *J. procera*) (Betemariam, 2011). The local communities use both *O. europaea* and *J. procera* in several ways, such as for farm implements, fuelwood, construction material, and medicine. In this study, we focus on these two species because they are threatened by over-exploitation and are considered locally endangered (Berhe and Negash, 1998; CBD, 2009; Negash, 2003; Viswanathan, 1986). Woldemichael et al. (2010) and Betemariam (2011) have previously studied vegetation structure in the study area, but we still lack information on how these two species relate ecologically to each other and to various biotic, abiotic and disturbance factors in the forest. Such knowledge is urgently needed for developing effective conservation measures.

This study examines how biotic, abiotic and disturbance factors influence the abundance and biomass of these two key dry Afromontane forest species. We pose three questions: (1) Is there a relationship between the abundance of *O. europaea* and *J. procera*? (2) How do abundance and biomass of these species correlate with biotic and abiotic variables? (3) Are the abundances of the two species affected by human disturbance?

2. Methods and materials

2.1. Study area

Hugumburda national forest priority area (12° 36′N, 39° 31′ E) is situated in southern Tigray, Ethiopia. Elevation ranges from 1860-2700 m above sea level. Average annual rainfall ranges from 800-1000 mm. Mean daily temperature is 14–22.4 °C, with a minimum of 8.8–10.7 °C in October and a maximum of 34.3 °C in June (Worku, 1998). The topography of the study area is mainly undulating to sharp terrain. Soils are shallow, with leptosols and regosols as the dominant soil types.

The total study area is ca. 8103 ha, and includes plantation forest, disturbed natural forest and some settlements and agricultural fields on the fringes of the forest. The area was previously densely forested with substantial numbers of the dominant indigenous plant species such as *Juniperus procera, Olea europaea* subsp.*cuspidata, Nuxia congesta, Cassipourea mallosana* and *Olinia rochetiana* (Betemariam, 2011; Sileshi and Abraha, 2014; Woldemichael et al., 2010). Although the forest is protected, making it illegal to cut trees, and is guarded by ca. 50 forest rangers, illegal logging still occurs.

2.2. Study species

Olea europaea occurs primarily in arid areas between 1250 and 3100 m a.s.l. Adult trees are commonly 15 m high, but can reach 25 m (Friis, 1992). The species occurs in marshy areas, dry lands, stony places and on mountain sides, where it tolerates a wide range of environmental conditions, including frost and drought (Bekele-Tesemma and Tengnäs, 2007). The wood is commonly used for fencing, making farm implements and manufacturing home furniture. The unique fragrance of the smoke of burnt *O. europaea* wood flavors and enhances traditional drinks and repels insects. The species is a medicinal plant in southeastern Ethiopia.

Juniperus procera is one of the characteristic tree species of dry Afromontane forests of Ethiopia. It is evergreen and can be up to 45 m tall at an age of 150 years. It is most abundant in the transition zone between dry and semi-evergreen forest. It often occurs together with *O. europaea* and *Podocarpus falcatus* (Berhe and Negash, 1998; Pohjonen and Pukkala, 1992). Its economic importance is considerable, being a raw material for home furniture, poles, fences and in the manufacture of lead pencils. Although globally categorized as a Least concern species (IUCN, 2017), *J.procera* suffers from widespread logging and its

population is declining in Ethiopia. Thus, it needs an in-situ strategy for conservation (Aynekulu et al., 2009; CBD, 2009; Negash, 2002; Viswanathan, 1986).

2.3. Field data collection

Seventy 20 × 20 m plots were positioned on forested slopes at elevations of 2233–2503 m a.s.l. The plots were distributed about 100 m apart along parallel transects placed perpendicular to three local terrain ridges, each transect running from the top to the bottom of the ridge. The distance between neighboring transects was ca. 150 m.

In each 20 × 20 m main plot, we identified, counted and recorded all adult trees and shrubs to species level. We measured stem diameter at breast height (DBH) of individual trees, basal diameter (BH) for each shrub, and the heights of both (West, 2009). The abundance and species identities of saplings were recorded in one 5 × 5 m sub-plot, placed in the center of each main plot. The number and identities of seedlings were recorded in five 1 × 1 m small plots, one placed in the center of each main plot and four at the corners of each 5 × 5 m sub-plot. We also visually determined the percent cover (to the nearest 1%) of herbaceous species within each 1 × 1 m small plot. For calculating species richness, we used plant height and diameter at breast height to classify each woody individual into adult, sapling or seedling: adults (DBH ≥ 2 cm), saplings (height ≤ 1.3 m and DBH ≤ 2 cm) and seedlings (height ≤ 0.3 m).

We sampled environmental conditions in the same plots as vegetation data. To quantify human disturbance, we used a tape measure to quantify the total length (m) of human footpaths in each main plot, using these tracks as one indicator of disturbance. We also counted the number of cut *O. europaea* stumps. Slope and elevation were measured in the center of each main plot with a clinometer and a handheld GPS respectively. For each of the 70 main plots, two separate soil samples were collected for soil moisture content (by soil core samplers) and chemical analysis. For soil chemical analysis we used a composite of five samples (top soil to 15 cm depth) collected at the center of each 1 × 1 m plot. The soil samples were sealed in a double plastic bag to preserve the soil moisture. All soil samples were transported to Mekelle Agricultural Research Center laboratory in Mekelle. Soil moisture was measured gravimetrically (Black et al., 1965). The composite soil samples were then air-dried at a room temperature and sieved through a 2-mm mesh. Soil pH (at 1:2.5 soil/H_2O), electrical conductivity and soil organic matter (Walkley-Black method) were measured using standard techniques (Nelson and Sommers, 1996). Soil depth was measured in the field by digging a pit at the center of the main plot down to bedrock.

2.4. Data analysis

2.4.1. Data preparation

To determine total woody species richness, we pooled all woody species (trees and shrubs) occurring in each main plot (adults), sub-plot (saplings) and small plots (seedlings). Woody species abundance was the number of adult individuals of each species counted in each main plot (expressed as a density, number per m²). Herbaceous cover was estimated as percentage cover and converted to proportions before data analyses.

The Above-ground biomass (AGB) of adult trees was calculated using the allometric equation developed by Chave et al. (2014).

$$AGB = 0.0673 * (WD *DBH^2 *H) \exp 0.976 \qquad (1)$$

Where WD = wood density (g/cm³), DBH = diameter at breast height (cm) and H = height (m).

For all tree species, we used an average wood density value of 0.612g/cm³ obtained from the global wood density database (Ministry Of Environment, 2016; Zanne et al., 2009).

2.4.2. Statistical analysis

The dataset was subjected to initial exploratory analyses following Zuur et al. (2010) to check for outliers and collinearity between candidate explanatory variables and to explore relationships between *O. europaea* and *J. procera* abundance and biomass and explanatory variables. To determine if there is a relationship between the abundance of *O. europaea* and *J. procera* trees, we fitted a generalized linear model, assuming a Poisson distribution of errors. However, this model was over-dispersed (generalized Pearson statistic gPs = 3.53). Therefore, we re-fitted the model with a negative binomial GLM (gPs = 0.95). Because of a strong correlation between *O. europaea* and *J. procera* abundance and biomass, we ran separate analyses for the two species to determine how the abundance and biomass of the two species were related to environmental conditions.

To reduce model complexity, we carried out a pre-selection of variables, fitting single-variable models for the relationship between 1) *O. europaea* abundance, 2) *O. europaea* biomass, 3) *J. procera* abundance and 4) *J. procera* biomass and each of the candidate biotic variables (woody species richness, total above-ground biomass of all tree species except *O. europaea* and *J. procera*, cover of herbaceous plants), abiotic variables (soil depth, soil pH, soil electrical conductivity, organic matter percentage, soil moisture, slope, elevation) and human disturbance variables (total track length, number of *O. europaea* stumps). Only explanatory variables that had a statistically significant influence ($p < 0.05$) on the response in single-variable models, were included in the full (most complex) models.

For the abundance response variables, we fitted negative binomial GLMs because Poisson GLMs were over-dispersed. For the biomass response variables, we fitted linear models, assuming normally distributed errors. To avoid collinearity, we made a correlation matrix with Pearson correlation coefficients (r) for all possible pairs of candidate explanatory variables. In cases where $r > 0.6$, we selected the variable most strongly correlated with the response (i.e., the highest r-value) for inclusion in the most complex model, while at the same time avoiding collinearity with other variables.

For *O. europaea* abundance, we initially fitted a full model with the main effects being woody species richness, herbaceous cover, number of *O. europaea* stumps, elevation and slope. We also included the quadratic term of herbaceous cover, to capture curvilinear relationships detected in the exploratory analyses. For *O. europaea* biomass, we first fitted a full model with tree biomass, track length, herbaceous cover, number of *O. europaea* stumps, and soil moisture as the main effects. We also included the quadratic terms of track length and herbaceous cover. As an outlier appeared to influence the track length response considerably, we re-run the model without the outlier. Then, track length was not significant anymore, whereas the other variables did not change. We decided to run the model without the outlier and thus without track length in the final model.

Initially, we did not consider *J. procera* abundance and biomass as response variables. However, during data exploration we found that *J. procera* was as dominant as the *O. europaea* trees in the forest, and we found that it had a strong relationship with *O. europaea*. Because *J. procera* is also a species of particular conservation interest, and to deal with the collinearity, we treated *J. procera* abundance and biomass as response variables in our analyses. For *J. procera* abundance, we fitted a full model with woody species richness, tree biomass, and elevation as the main effects. For *J. procera* biomass, we initially fitted a full model with the main effects being tree biomass and number of *O. europaea* stumps.

We carried out model selection by backward elimination, sequentially deleting non-significant terms (likelihood ratio test, $p < 0.05$) (Crawley, 2013). The variance inflation factor (VIF) values were < 5 for all combinations of the explanatory variables in the final models. Graphical validation of the final models indicated adequate fit. We used the R 3.2.5 software for all analyses (R-Development Core Team, 2016).

2.4.2.1. Olea europaea and J. procera abundance and community composition of woody species.
Non-metric Multidimensional Scaling (NMDS) was performed to investigate the association between the abundance of *O. europaea* and *J. procera*, the environmental variables that influenced these response variables in the GLMs, and community composition of woody species. NMDS was based on Jaccard dissimilarity matrix calculated from the presence-absence of adult tree and shrub species in each plot. We used the metaMDS function in the vegan package in R (Oksanen et al., 2013), with 1000 random starting points. The squared correlation coefficient (R^2) was used to define the relationship between the environmental gradients and ordination axes scores. The importance of each environmental variable was assessed from the squared correlation coefficient (R^2) between the environmental variable and the ordination axes, and the significance of factor variables was assessed using R^2 as a goodness-of-fit statistic for the whole factor. The statistical significance (p-values) of both vector and factor variables was based on random permutations of the data. To assess which environmental variables (woody species richness, tree biomass, *J. procera*, *O. europaea* and elevation) had most influence on species composition, we used the envfit command to fit vectors (continuous variables) of environmental variables onto the NMDS ordination. To choose an appropriate number of dimensions (k), we performed ordinations of progressively higher dimensions ($k = 2$ to $k = 5$), which produced stress values of 0.212, 0.151, 0.118 and 0.094, respectively. We opted to represent our data in three dimensions (linear fit: $R^2 = 0.85$) to lessen complexity.

3. Results

3.1. Abundance and aboveground biomass relationship between O. europaea and J. procera

The abundances of *O. europaea* and *J. procera* were positively correlated, with the abundance of *O. europaea* doubling when the number of *J. procera* increased from zero to 15 per plot (Fig. 1a).

The aboveground biomass of *O. europaea* was also positively linearly related to that of *J. procera* (Fig. 1b). When *J. procera* biomass increased from zero to 50 kg per plot, *O. europaea* biomass increased at half that rate.

3.2. Factors influencing O. europaea abundance

The negative binomial model explained 42% of the variation in the abundance of *O. europaea* (Table 1). We found a significant positive relationship between *O. europaea* abundance and woody species richness, herbaceous cover, elevation, slope, and number of *O. europaea* stumps, although the influence of herbaceous cover levelled off when it exceeded ca. 25% (Table 1, Fig. 2). For example, with an increase in woody species richness from 10 to 20, the abundance of *O. europaea* doubled. *Olea europaea* was more abundant at higher elevations and on steeper slopes.

3.3. Factors influencing O. europaea biomass

The linear regression model explained 45% of the variation in *O. europaea* biomass (Table 2). *O. europaea* biomass was positively correlated with total aboveground tree biomass, herbaceous cover (%), soil moisture, and *O. europaea* stumps (Table 2 and Fig. 3). For instance, *O. europaea* biomass increased by 10 kg/plot when the amount of total aboveground tree biomass increased from zero to 50 kg/plot. *O. europaea* biomass was also positively related to the number of *O. europaea* stumps.

3.4. Factors influencing J. procera abundance

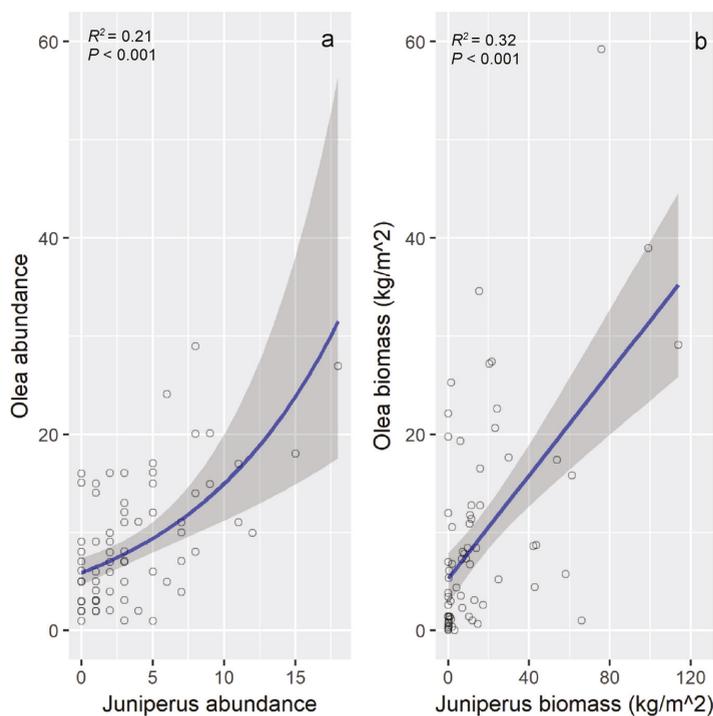The negative binomial model explained 45% of the variation in the

Fig. 1. The relationship between abundance (a, negative binomial model) and biomass (b, linear regression model) of *J. procera* and *O. europaea* in Hugumburda dry Afromontane forest in northern Ethiopia. The solid lines indicate the fitted lines and the shaded polygons are the 95% confidence intervals. Open circles show observed values.

Table 1

Factors influencing *O. europaea* abundance in Hugumburda dry Afromontane forest in northern Ethiopia. The table shows parameter estimates and associated standard errors for a negative binomial model of the relationship between *O. europaea* abundance and the explanatory variables retained in the final model ($R^2 = 0.42$).

	Estimate	SE	z	P
Intercept	−7.50	2.80	−2.7	0.006
Woody species richness	0.08	0.02	2.5	0.010
(Herbaceous cover)^2	−7.60	3.30	−2.3	0.021
Herbaceous cover (%)	3.40	1.60	2.1	0.032
Elevation (m)	0.01	0.00	2.8	0.005
Slope (˚)	0.96	0.32	3.0	0.002
Number of *O. europaea* stumps	0.09	0.02	4.0	< 0.001

abundance of *J. procera* (Table 3). The abundance of *J. procera* was positively related to woody species richness, tree biomass and elevation (Table 3, Fig. 4). For instance, the abundance of *J. procera* tripled when tree biomass increased from 50 to 200 kg/plot. The abundance of *J. procera* doubled when total richness increased from 10 to 20 per plot.

3.5. Factors influencing J. procera biomass

The linear regression model explained 27% of variation in *J. procera* biomass in Hugumburda forest (Table 4). There was a positive relationship between *J. procera* biomass and woody species richness and elevation (Fig. 5). *J. procera* biomass doubled when woody species richness increased from 13 to 20, and *J. procera* biomass also increased when elevation increased.

3.6. Relationships among variables overall

The ordination plot (Fig. 6) shows the co-occurrence of shrub and tree species composition along the environmental gradients, and their association with *O. europaea* and *J. procera*. All variables: *O. europaea*, *J. procera*, woody species richness, elevation and tree biomass correlated with the three first NMDS axes (Table 5). The shrubs *Dodonaea angustifolia* and *Euclea racemosa* (both pioneers), *Jasminum congesta* and *Heteromorpha trifoliata*, and the tree species *Teclea simplicifolia* and *Pittosporum viridiflorum*, are strongly associated with both *O. europaea* and *J. procera* abundance in the forest. Conversely, tree species like *Cupressus lusitanica*, *Maytenus undata* and *Olinia rochetania* and the shrub *Calpurnia aurea* were negatively associated with both *O. europaea* and *J. procera* abundance (Fig. 6).

4. Discussion

We found a positive relationship between the abundance and biomass of *J. procera* and *O. europaea*. This is relevant for conservation, as it suggests that there is no negative relationship between them, and thus the dominance of one will likely not threaten the other. We hypothesize that this pattern may be due to facilitation (Gómez-aparicio, 2009), which could promote co-existence of these two dominant trees. Experiments by Aerts et al. (2006a) show that *O. europaea* is shade-tolerant, whereas *J. procera* is shade-intolerant (Aynekulu et al., 2009). Thus, it is possible that *J. procera* provides shade for *O. europaea*, thereby facilitating its abundance in this dry environment (Yirdaw, 2001). Michelsen et al (1993) also reported that soils in areas dominated by *J. procera* are relatively nutrient rich. An alternative hypothesis is that niche partitioning between these two species explains their coexistence and high abundance of both species (Valladares et al., 2015). Niche partitioning might take place between abundant tree
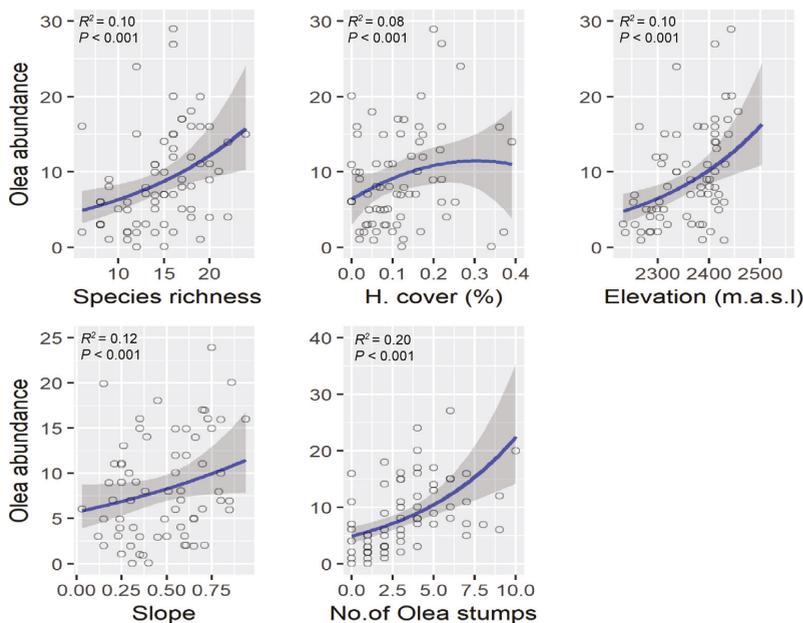
Fig. 2. Estimated relationships between *O. europaea* abundance and biotic, abiotic and human disturbance factors in Hugumburda. Figures show results from negative binomial models. The solid lines show estimated relationship between the response variable and each of the explanatory variables, in single-variable models with only one explanatory variable. The shaded polygons are the associated 95% confidence intervals. Open circles show observed values.

Table 2

Factors influencing *O. europaea* biomass in Hugumburda. The table shows results from a linear regression model fit between aboveground *O. europaea* biomass and the explanatory variables retained in the final model ($R^2 = 0.45$).

	Estimate	SE	t	P
Intercept	−7.36	2.84	−2.6	0.006
Tree biomass (kg/m²)	0.09	0.03	3.0	0.004
(Herbaceous cover)²	−116.80	38.87	−3.0	0.004
Herbaceous cover (%)	55.03	19.06	2.9	0.005
Soil moisture (g)	0.20	0.08	2.4	0.020
Number of *O. europaea* stumps	1.52	0.28	5.4	< 0.001

species in arid areas, suggesting that the two abundant tree species coexist because they have different resource requirements (Fetene and Feleke, 2001; Hubbell, 1980; Peterson et al., 2013).

Our results also show a positive relationship between both the abundance and biomass of *J. procera* and *O. europaea* and woody species richness. Based on this, woody species richness may enhance the abundance of these two species by ameliorating environmental conditions. After disturbance in arid areas, early successional species, such as *Dodonaea angustifolia* and *Euclea racemosa*, could increase soil fertility and ameliorate the environment by providing shade and soil moisture for late succession species, such as *O. europaea* and *J. procera* (Gómez-aparicio et al., 2004; Zanini and Ganade, 2005)? We also observed a significant positive relationship in our study area between soil moisture content and *O. europaea* biomass. This could be due to shading resulting from the combined influence of abundant *O. europaea* trees and other species, as reflected in high woody species richness. Maestre et al. (2012) showed that woody species richness can positively influence abiotic environmental factors, for instance by increasing soil fertility through facilitating carbon and nitrogen cycling in dry forest ecosystems. Similar processes could explain the positive relationship between woody species richness and the abundance of *O. europaea* and *J. procera* in our study area. In contrast (Shirima et al., 2015), suggest that dominant tree species had a negative effect (competition) on woody species richness in Miombo woodland in Tanzania. This is, however, a

wetter and thereby less stressful ecosystem than our arid study area. In line with the stress-gradient hypothesis, suggesting facilitation being more common in conditions of high abiotic stress relative to more benign abiotic conditions, where competition is more prevalent (Maestre et al., 2009), we hypothesize that facilitation might be more important than competition in determining plant species co-occurrence in arid systems such as Hugumburda.

We found a positive relationship between herbaceous cover and *O. europaea* abundance up to ca. 25% cover; thereafter it levelled off. A forest dominated by *J. procera* has high soil nutrient content (Michelsen et al. (1993). Improved soil fertility could enhance the growth of herbaceous plants (Berhe and Negash, 1998; Jennings et al., 1999), but in areas of greater tree density, where canopy gaps are fewer and smaller, low light levels may reduce ground cover and seedling growth. This could explain why herbaceous cover levelled off where *O. europaea* was abundant, perhaps indicating overall high abundance of overstorey plant species generally, including *O. europaea* and *J. procera* (Yirdaw, 2001).

We found a positive relationship between the abundance of *O. europaea* and elevation and slope. *J. procera* abundance was also positively related to elevation. This suggests that topographic factors such as slope and elevation may play a significant role in the distribution of *O. europaea* and *J. procera* in these mountains (Måren et al., 2015; Mehnatkesh et al., 2013). Abiotic factors such as soil depth and moisture may in turn be affected by elevation. For instance, shallow soil depth was observed at higher elevations in the same study area (Betemariam, 2011). This could mean a lower soil moisture content at higher elevations because of shallow soils and rocky ground, although the positive relationship between *O. europaea* abundance and soil moisture suggests a canopy effect (microclimate improvement) by woody species on the surrounding soil (Gómez-aparicio et al., 2005). Alternatively, the abundance of deep-rooted tree species, such as *J. procera* and *O. europaea*, may increase with elevation because they can grow on rocky ground at higher altitudes and withstand the dry climate better than shallow-rooted species (Aerts et al., 2006b; T. Bekele, 2000; Wubet et al., 2003).
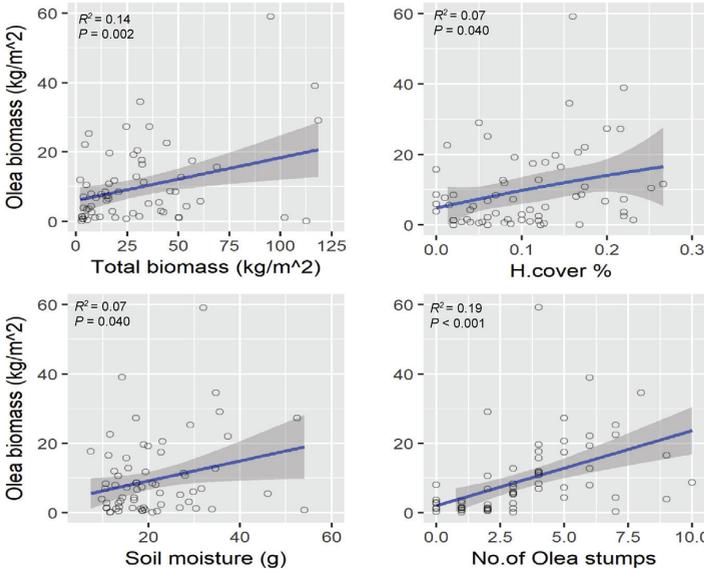
Fig. 3. Relationships between aboveground *O. europaea* biomass and biotic, abiotic and human disturbance factors in Hugumburda. Figures show results from linear regression models. Solid lines show estimated relationship between the response variable and each of the explanatory variables, in single-variable models with only one explanatory variable. The shaded polygons are the associated 95% confidence intervals. Open circles show observed values.

Table 3

Factors influencing *J. procera* abundance in Hugumburda. The table shows parameter estimates and associated standard errors for a negative binomial model of the relationship between *J. procera* abundance and the explanatory variables retained in the final model ($R^2 = 0.45$).

	Estimate	SE	Z	P
Intercept	−13.78	4.36	−3.2	0.001
Woody species richness	0.06	0.03	2.2	0.030
Tree biomass (kg/plot)	0.01	0.01	3.0	0.003
Elevation (m.a.s.l.)	0.01	0.01	3.1	0.001

Table 4

Factors influencing *J. procera* biomass in Hugumburda. The table shows a summary of statistical estimates from a simple linear regression model fit between aboveground *J. procera* biomass and the explanatory variables retained in the final model ($R^2 = 0.27$).

	Estimate	SE	t	P
Intercept	−340.7	90.70	−3.8	< 0.001
Woody species richness	1.4	0.60	2.2	0.030
Elevation (m.a.s.l.)	0.1	0.04	3.6	< 0.001

influence the abundance of *O. europaea* and *J. procera*.

5. Conclusion and implication for management

As our study was not experimental, we cannot conclude with any causal relationships of the observed patterns. However, based on our observations, we suggest that conserving woody species richness would promote the conservation of the two multi-purpose tree species as well as the entire forest. The positive relationship between the abundance of *O. europaea* and cut stumps showed that selective illegal logging is common in *O. europaea*-rich areas in the forest. Controlling this could help the forest administrators conserve forest resources more widely.

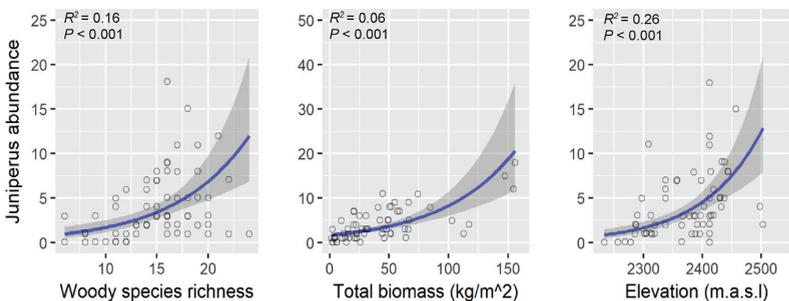Based on our findings, therefore, we conclude that the management

Both the biomass and the abundance of *O. europaea*, and the number of cut *O. europaea* stumps in the forest were positively correlated. This may suggest that the local community mainly cut stumps in dense stands of *O. europaea,* and is in line with the findings of (Kidane et al., 2016; Woldemichael et al., 2010), who documented intensive illegal harvesting of *O. europaea* occurring in the forest. Human activities, such as forest clearance for agriculture and illegal harvesting, are the main drivers of land-use change from primary to secondary forests (Mcgill, 2015; Newbold et al., 2015). Illegal harvesting was the main form of human disturbance in Hugumburda. Further research is needed to understand how other disturbance factors, such as grazing intensity, fuelwood collection and expansion of farmland into the forest reserve,

Fig. 4. Relationships between *J. procera* abundance and biotic and abiotic factors in Hugumburda. Figures show results from negative binomial models. Solid lines show estimated relationship between the response variable and each of the explanatory variables, in single-variable models with only one explanatory variable. The shaded polygons are the associated 95% confidence intervals. Open circles show observed values.
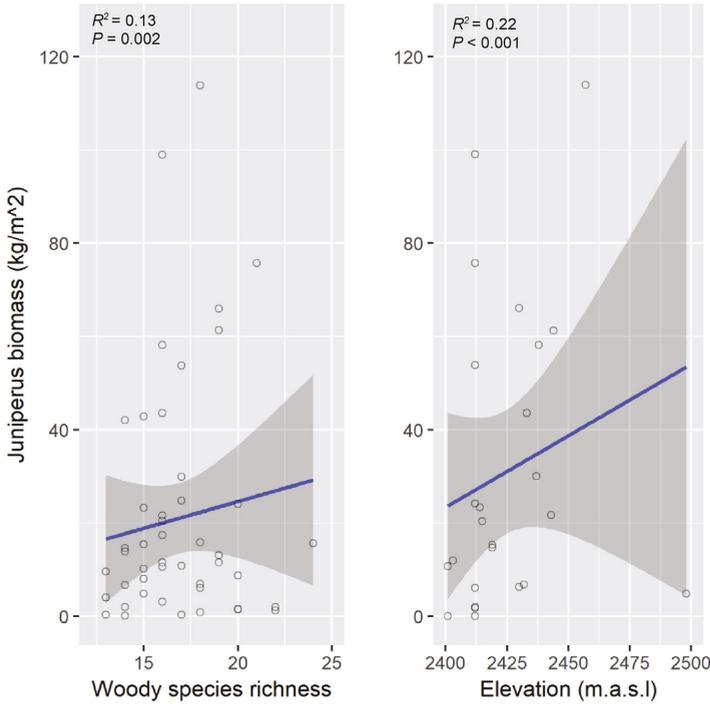
Fig. 5. Relationships between *J. procera* biomass and woody species richness and elevation in Hugumburda. Figures show results from linear regression models. Solid lines show estimated relationship between the response variable and each of the explanatory variables, in single-variable models with only one explanatory variable. The shaded polygons are the associated 95% confidence intervals. Open circles show observed values.
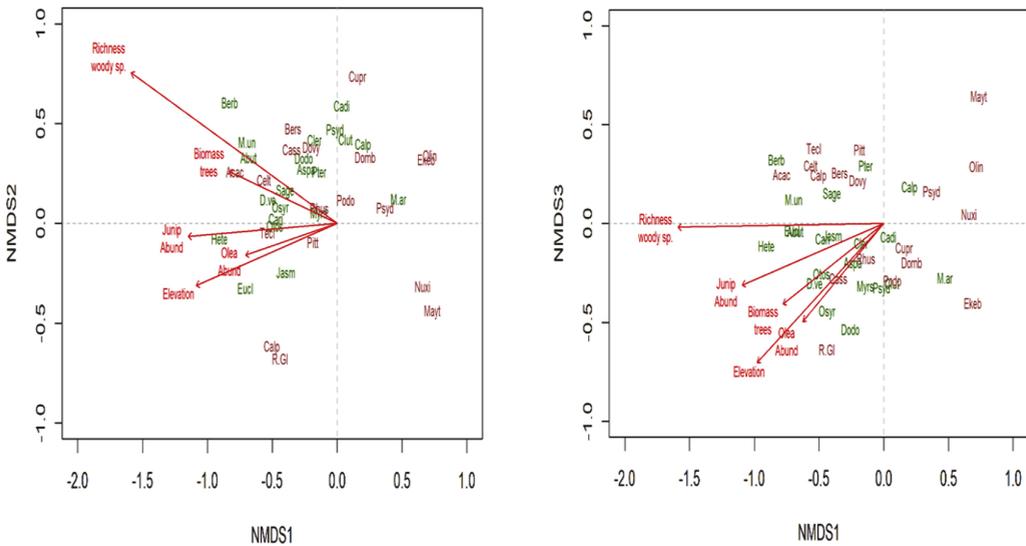

Fig. 6. Nonmetric multidimensional scaling (NMDS) ordination of environmental gradients versus species composition. Environmental gradients are shown in red, tree species in brown, shrub species in dark green. *Acacia abyssinica* (Acac), *Berberis holstii* (Berb), *Bersama abyssinica* (Bers), *Cadia purpurea* (Cadi), *Calpurnia aurea* (Calp), *Carissa edulis* (Cari), *Cassipourea malosana* (Cass), *Celtis africana* (Celt), *Clerodendron myricoides* (Cler), *Clutia abyssinica* (Clut), *Cupressus lusitanica* (Cupri), *Dovyalis verrucosa* (D.ve), *Dodonaoea angustifolia* (Dodo), *Dombeya torrida* (Domb), *Dovyalis abyssinica* (Dovy), *Ekebergia capensis* (Ekeb), *Euclea racemosa* (Eucl), *Heteromorpha trifoliata* (Hete), *Jasminum congesta* (Jasm), *Juniperus procera* (Juni), *Maytenus arbutifolia* (M.ar), *Maytenus undata* (May), *Maytenus undata* (May), *Myrsine africana* (Myrs), *Nuxia congesta* (Nuxi), *Olea europaea* (Olea), *Olinia rochetania* (Olin), *Osyris quadripartite* (Osyr), *Otostegia fruticosa* (Otos), *Pittosporum viridiflorum* (Pitt), *Podocarpus falcatus* (Podo), *Psydrax schimperiana* (Psyd), *Pterolobium stellatum* (Pter), *Rhus glutinosa* (R.Gl), *Rhus natalensis* (Rhus), *Sageretia thea* (Sage) and *Teclea simplicifolia* (Tecl). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 5

Squared correlation coefficients and associated P-values from permutation tests of the associations between *O. europaea* abundance, *J. procera* abundance, environmental gradients and NMDS axes.

Environmental Variables	NMDS 1 Vs NMDS 2		NMDS 1 Vs NMDS 3	
	r^2	P	r^2	P
O. europaea abundance	0.079	0.057	0.126	0.010
J. procera abundance	0.222	0.001	0.257	0.002
Woody species richness	0.511	0.001	0.433	< 0.001
Tree biomass (kg/plot)	0.145	0.007	0.174	0.002
Elevation (m.a.s.l.)	0.309	0.001	0.314	< 0.001

plan for conserving endangered tree species in dry montane forests should include the consideration for conserving other woody species, which in turn would promote the abundance of both locally endangered tree species.

Acknowledgment

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Paper II

Ontogenetic niche shifts in a locally endangered tree species (*Olea europaea* subsp. *cuspidata*): implications for conservation

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ABSTRACT

Studying the response of different ontogenetic stages to environmental and human disturbance factors is vital for applying conservation strategies to endangered plant species. We studied the ontogenetic niche shifts between life stages of a locally endangered tree species, *Olea europaea* subsp. *cuspidata* in relation to such factors in Hugumburda dry Afromontane forest in Ethiopia. Individual seedlings, saplings and adults of *O. europaea* were counted in 70 20 m x 20 m quadrats distributed over ca. 2.8 ha. We also measured biotic (woody species richness, canopy cover, aboveground tree biomass, herbaceous cover), abiotic (soil and topographic variables), and human disturbance factors (logging and tracks). We used a novel analytic approach, comparing both empirical and simulated observations as input data. The resulting ordination and logistic regression analyses showed that the probability of finding *O. europaea* seedlings, saplings and adults related differently to woody species richness, soil depth, slope and logging, suggesting ontogenetic niche shifts. The probability of finding *O. europaea* seedlings increased with increasing soil depth. The probability of finding *O. europaea* saplings appeared to increase with woody species richness and decrease on steeper slopes, whereas the probability of finding adults increased on steeper slopes and with logging. The population structure of *O. europaea* shows low recruitment, with few seedlings per hectare compared with the densities of saplings and adults. We conclude that our approach of using both empirical and simulated observations to detect ontogenetic niche shifts may be useful in plant population studies. We also suggest that the observed niche requirements of the different lifestages of *O. europaea*, together with the low regeneration status, should be considered when conservation strategies are developed for this species. Seedlings especially should be protected from browsing.

INTRODUCTION

Niche requirements of plants may change through their different life stages (Parish & Bazzaz, 1985; Miriti, 2006). One reason could be differences in micro-site suitability for the various life stages of the same plant population. For instance, the requirements of seedlings (i.e. the regeneration niche) can differ from that of later life stages (Grubb, 1977; Poorter, 2007). According to the regeneration niche hypothesis, such ontogenetic niche shifts start with niche differentiation, which takes place early in a plant's life (Weng, Yang, Hsieh, Hsieh, & Su, 2017). Regeneration niches of the plant population is determined by the availability of viable seeds, the abundance of seedlings, and the intensity of light reaching the ground, together with other biotic, abiotic and disturbance factors (Silvertown, 2004; Quero, Gómez-Aparicio, Zamora, & Maestre, 2008; Larpkern, 2010). In contrast, according to the unified neutral theory (Rosindell, Hubbell, & Etienne, 2011), niche shifts in plants are less relevant, because plants, unlike animals, commonly share similar resources from the environment (Chave, 2004). Thus, the concept of ontogenetic niche shifts has been less-well studied in plant ecology (but see Parish & Bazzaz, 1985; Miriti, 2006; Quero et al., 2008; Lucas-Borja, Fonseca, Linares, Morote, & Serrano, 2012). In contrast, niche shifts between consecutive stages is common and well-studied in animals (Valeix, Chamaillé-Jammes, & Fritz, 2007; Subalusky, Fitzgerald, & Smith, 2009). The reasons are complex but perhaps reflect the difference that unlike many animals, which are mobile and can move to environments that suit their needs at different developmental stages, plants are sessile and must adjust at each stage to the environment in which they find themselves. Ontogenetic niche shifts in plants therefore reflect the intersection of changes in environments over time; developmental changes in the plants as they mature, and whether these expand or contract a

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species' niche space; and any resulting differentials among individuals in growth rates and survival.

Examining the responses of different ontogenetic stages to abiotic and biotic environmental and disturbance factors may give insights into how niche shifts can occur between different life stages of the same plant species (Mikkelson, 2005; Wendelberger & Maschinski, 2016). For instance, in an ontogenetic niche shift experiment on three *Vaccinium* shrub species in a boreal forest, the niche requirements of juvenile *Vaccinium vitis-idaea*. L were different from those of adults (Eriksson, 2002). Studies that include sequential life stages are therefore important for understanding plant population dynamics and applying this knowledge to conservation measures (Quero et al., 2008). In addition, environmental factors play a significant role in ontogeny niche shifts and are further important in understanding plant distribution and abundance (Wasof et al., 2013; Cornuault, Khimoun, Cuneo, & Besnard, 2015). For instance, in a study of 12 montane-forest tree species in Slovakia, the abundance of seedlings varied significantly from those of saplings and adults in response to elevation, temperature, and precipitation (Malis, Kopecky, Petrik, Vladovic, Merganic, & Vida, 2016). Environmental factors can also limit niche shifts in exotic plant invasions and distribution (Gabler & Siemann, 2012). Understanding how biotic, abiotic and human disturbance factors influence ontogenetic niche shift dynamics within a plant population therefore becomes vital for developing effective conservation strategies (Quero et al., 2008).

Most previous studies of ontogenetic niche shifts in plants have used analysis of variance or generalized linear (mixed) model approaches (Eriksson, 2002; Quero et al., 2008; Lucas-Borja et al., 2012; Wendelberger & Maschinski, 2016; Müller, Albach, & Zotz, 2018). In contrast, Larpkern (2010) and Schurman & Baltzer (2012) used canonical correspondence analysis to analyze whether various ontogenetic stages differed in their response to environmental conditions. Comparing observed abundances among life stages is not

straightforward because the sizes of individuals differ substantially as they mature. To overcome this problem, we applied a novel analytic approach, using both empirical and simulated observations (random relocations of the observed data) as inputs.

In this paper, we report the population structure and ontogenetic niche shifts of a locally endangered tree species, *Olea europaea* subsp. *cuspidata* (hereafter *O. europaea*). This is an important species to study ontogenetic niche shifts because of its ability to grow in dry and moist environments (Kassa, Konrad, & Geburek, 2018). It is locally endangered because of overexploitation for wood for multiple purposes (Sileshi & Abraha, 2014; Kassa, Konrad, & Geburek, 2017) and needs conservation. We asked the following questions: (i) What is the current structure of the *O. europaea* population in the forest? (ii) How are the various life stages of *O. europaea* related to different environmental factors? (iii) Can the niche of adult *O. europea* be predicted by the same environmental variables as those for saplings and seedlings?

MATERIALS AND METHODS

Study species and area

In Ethiopia, *Olea europaea* subsp. *cuspidata* occurs mostly in dryland areas between 1250 to 3100 m a.s.l. The height of adult trees rarely reaches 25 m (Friis, 1992; Negash, 2004). Once established, the tree grows well in both warm and cold climate conditions (Bekele-Tesemma & Tengnäs, 2007). *O. europaea* wood is commonly used for fencing, fuelwood and making charcoal, and for manufacturing farm implements and home furniture. Because of its multipurpose use, the species has become locally endangered in Ethiopia (Viswanathan, 1986; Negash, 2003; Kassa et al., 2017, 2018).

The study area is in Hugumburda dry Afromontane forest (12^0 22'–12^0 42' N, 39^0 28'–39^0 40' E), which is one of the National Forest Priority Areas, located Tigray Province in the northern part of Ethiopia. Elevation ranges from 1796–2772 m above sea level. Mean

annual temperature is 15.4 $^\circ$C with a daily temperature range from 14.6 to 22.4 $^\circ$C. With a mean minimum temperature of 10.7 $^\circ$C, October is the coldest month. June is the hottest, with a mean maximum of 34.3 $^\circ$C (Woldemichael, Bekele, & Nemomissa, 2010). Mean annual rainfall is 705 - 986 mm (Kidane, Nemomissa, & Bekele, 2018). Our study area covered ca. 2.8 ha of the forest, comprising high-elevation natural forest and plantations. The structure of the forest mainly comprises trees, bushes, lianas, and herbs. Dominant woody species are *Juniperus procera*, *Olea europaea* subsp. *cuspidata*, *Nuxia congesta, Rhus glutinosa, R. natalensis*, and *Olinia rochetania* (Woldemichael et al., 2010). Although the forest is legally protected, there is still illegal wood collection and cattle grazing.

Field data collection

Seventy 20 × 20 m plots were placed on forested slopes at elevations of 2233–2503 m a.s.l. The plots were distributed about 100 m apart along parallel transects placed perpendicular to three local terrain ridges, each transect running from the top to the bottom of the ridge. The distance between neighboring transects was ca. 150 m (see Wegasie et al., 2018).

In each 20 × 20 m main plot, we measured stem diameter at breast height (DBH) and the heights of all adult *O. europaea* individuals (West, 2009). The abundance, height and diameter of *O. europaea* saplings were recorded in 5 × 5 m sub-plots, placed in the center of each main plot. The number and heights of *O. europaea* seedlings were recorded in five small 1 × 1 m plots, one placed in the center of each main plot and four at the corners of the 5 × 5 m sub-plots. To classify life stages of *O. europaea* into adult, sapling or seedling we used the following criteria: adults (DBH > 2 cm, irrespective of height, to account for cut stumps); saplings (height $0.4 \leq 1.3$ m and DBH < 2 cm) and seedlings (height ≤ 0.3m).

We sampled biotic, abiotic and human-disturbance variables in the same plots as the vegetation data. For biotic factors, we recorded the number of woody species (woody-species richness) and the height and DBH of these trees, from which we calculated aboveground biomass (hereafter biomass). Tree canopy cover was estimated visually as percentage cover to the nearest 1%. We also visually determined the percentage cover of herbaceous species in each 1×1 m plot.

Slope and elevation were measured in the center of each main plot with a clinometer and a handheld GPS, respectively. For each of the 70 main plots, a soil core sampler was used to collect two separate, surface to 15-cm depth, soil samples: one for measuring soil moisture content; the other for chemical analysis. For the soil chemical analyses, we used a composite of five samples collected at the center of each 1×1 m plot. The soil samples were sealed in a double plastic bag to preserve the moisture. All soil samples were transported to Mekelle Agricultural Research Center laboratory in Mekelle. Soil moisture was measured gravimetrically (Gardner, 1965). The composite soil samples were air-dried at a room temperature and sieved through a 2-mm mesh. Soil pH (a 1:2.5 soil:H_2O mixture) and soil organic matter (Walkley-Black method) were measured using standard techniques (Nelson & Sommers, 1996). Soil depth was measured in the field by digging a pit at the center of the main plot down to bedrock.

To quantify human disturbance in each main plot, we measured the total length (m) of human footpaths (hereafter tracks) with a measuring tape, and estimated logging by counting the number of cut *O. europaea* stumps (hereafter logging). We used these variables as indicators of human disturbance.

Data analysis

Data preparation

To assess *O. europaea* population structure, we sorted all the individuals into 14 diameter and 12 height classes. The diameter classes expanded at 1.2 cm increments from class 1 ($\leq$ 0.7 cm) to 14 ($\geq$ 16.3 cm). The height classes increased at 0.9 m increments from class 1 ($\leq$ 0.3 m) to 12 ($\geq$ 10.3 m). The number of individuals in each class was calculated and the diameter and height distributions presented as frequency histograms.

We calculated the above-ground biomass (AGB) of all adult tree species found in the main plots by applying DBH, height (H) and wood density (WD) to the following allometric equation developed for tropical trees (Chave et al., 2014):

$$AGB = 0.0673 * (WD * DBH^2 * H)^{0.976}$$

Average wood density (0.612 g/cm^3) for all tree species was obtained from the global wood density database (Zanne et al., 2009).

Statistical analyses

We used Non-metric Multidimensional Scaling (NMDS) to investigate the associations between life stage (seedlings, saplings and adults), and the environmental and disturbance factors. All environmental variables and the abundance of individuals in each life stage were standardized to make them comparable. The Bray Curtis dissimilarity index was used to define an appropriate number of dimensions (k) in the NMDS analyses. We performed ordinations of progressively higher dimensions (k = 2 to k = 4), which produced stress values of 0.215, 0.151 and 0.110, respectively. The NMDS analyses were done through the metaMDS function in the vegan package in R (Oksanen, Blanchet, Kindt, et al., 2013), with 1000 random starting points. The importance of each environmental variable was assessed from the squared correlation coefficient (R^2) between the environmental variable

and the ordination axes. Statistical significance (p-value) of both vector and factor variables was based on random permutations of the data. To assess which life stages of *O. europaea* abundance (as environmental gradients) were associated with specific environmental factors (biotic, abiotic and human disturbance), we used the envfit command to place the vectors (i.e. the abundance of life stages) of environmental gradients onto the NMDS ordination. To reduce complexity, we limited our data presentation to three dimensions (linear fit: $R^2 = 0.84$).

NMDS—like other ordination techniques—indicates differences among seedlings, saplings and adults in their association with the various environmental factors but it does not provide a valid statistical test of the strength of these associations. Therefore, we compared our empirical data with a simulated dataset consisting of random relocations of the sampled seedling, saplings and adult individuals from the 70 plots. The dataset of randomly relocated individuals was simulated with the reshape2 package in R.

To determine if the abundances of seedlings, saplings and adults were influenced by the same explanatory variables, we fitted a general linear model (GLM) with a binary response in which $Y = 0$ for simulated observations, and $Y = 1$ for empirical observations. We assumed a binomial distribution of errors and used a logit link function (logistic regression). The model estimated the likelihood of an empirical observation responding to the explanatory variables. Hereafter, we refer to the response variable as the probability of finding *O. europaea.* To reduce model complexity, we pre-selected variables by fitting single variable models between this response variable and each of the candidate explanatory variables, for each ontogenetic stage. Candidate explanatory variables included both biotic (woody species richness, total aboveground biomass of all tree species except *O. europaea*, canopy cover and cover of herbaceous plants), abiotic (soil depth, soil pH, organic matter percentage, soil moisture, slope, elevation) and human disturbance variables (tracks and

logging). We fitted a full model with those explanatory variables that were significantly related (p < 0.05) to the response variable for at least one of the ontogenetic stages, using the two-way interactions between each of these variables and the three ontogenetic stages as explanatory terms. A significant interaction (p < 0.05) between an ontogenetic stage and an environmental variable was interpreted as indicating a difference among the ontogenetic stages in their response to the environmental variable, thus signifying an ontogenetic niche shift.

We carried out model selection by stepwise variable selection, adding or removing predictors to produce a model that minimized Akaike's information criterion (AIC). The general variance inflation factor (GVIF) values were < 5 for all combinations of the explanatory variables in the final models. The model was fitted using the MASS package in R 3.2.5 software (R-Development Core Team, 2016).

RESULTS

Olea europaea population structure

The abundance of *O. europaea* seedlings (7 ± 5 individuals ha^{-1}) was much less than either the sapling (79 ± 25 individuals ha^{-1}) or adult stages (219 ± 39 individuals ha^{-1}). The diameter distribution of the population also indicated that the number of seedlings was low compared with the older sapling and adult stages. Most individuals were found in diameter classes 2–9 (Fig. 1) and in height classes 2–7 (Fig. 2). There was a sharp decline in number of individuals higher than 5.3 m (height classes 7 and above, Fig. 2).
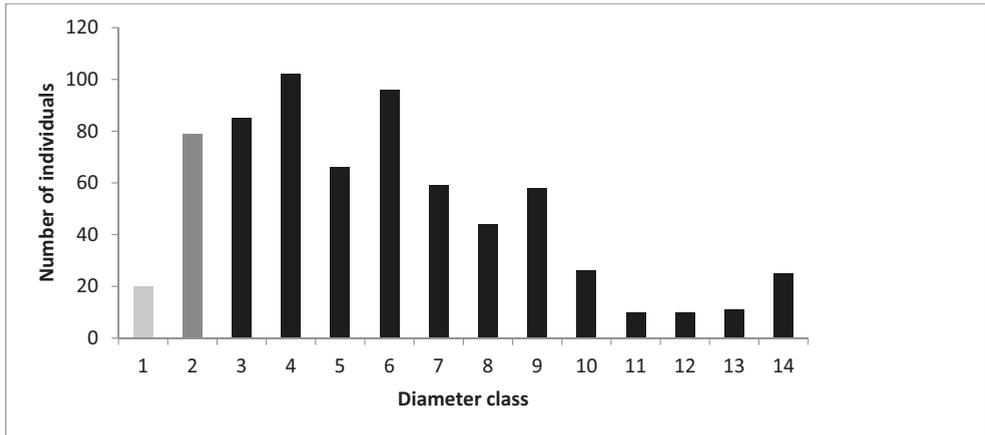
Fig. 1. Diameter class distribution of *O. europaea* subsp. *cuspidata* in Hugumburda forest (1 = < 0.8, 2 = 0.8–2.0, 3 = 2.1–3.3, 4 = 3.4–4.6, 5 = 4.7–5.9, 6 = 6–7.2, 7 = 7.3–8.5, 8 = 8.6–9.8, 9 = 9.9–11.1, 10 = 11.2–12.4, 11=12.5–13.7, 12 = 13.8–15.0, 13 = 15.1–16.3 and 14 >16.3 cm). Seedlings, light grey bar; saplings, dark grey bar; and adult trees, black bars.
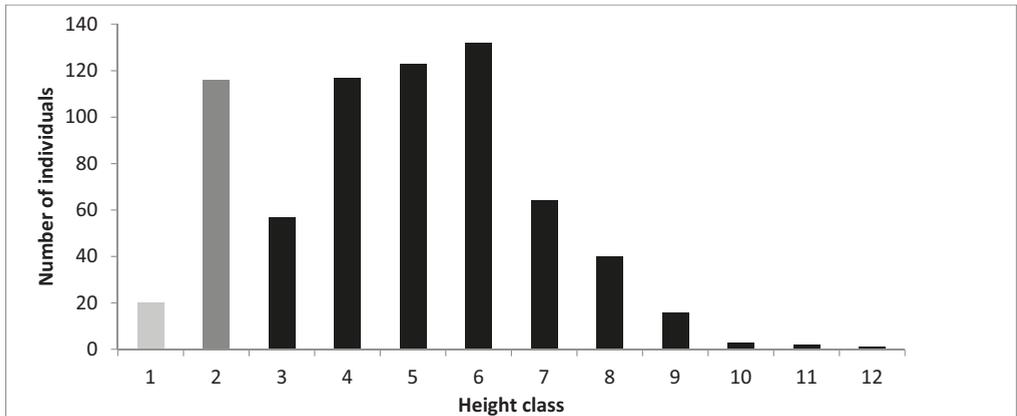

Fig. 2. Height class distribution of *O. europaea* subsp. *cuspidata* in Hugumburda forest (1 < 0.4, 2 = 0.4–1.3, 3 = 1.4–2.3, 4 = 2.4–3.3, 5 = 3.4–4.3, 6 = 4.4–5.3, 7 = 5.4–6.3, 8 = 6.4–7.3, 9 = 7.4–8.3, 10 = 8.4–9.3, 11 = 9.4–10.3, 12 = > 10.3 m). Seedlings, light grey bar; saplings, dark grey bar; and adult trees, black bars.

Relationships between *O. europaea* life-stages and environmental variables

The NMDS ordination plots show the pattern of association of the seedling, sapling and adult life stages of *O. europaea* with their environment. *O. europaea* seedlings were not significantly associated with any of the NMDS axes. In contrast, saplings and adults were, but in different ways. Saplings were evidently related to the second and third NMDS axes (positively associated with elevation and herbaceous cover on NMDS 2, and with organic matter on NMDS 3, and negatively associated with logging, slope and tracks on both axes: Table 1 & Fig. 3). Conversely, adults seemed to be positively associated with slope, slightly less positively linked with herbaceous cover and logging, and negatively associated with tracks and pH, all on NMDS 3 (Table 1 & Fig. 3).

Table 1. Squared correlation coefficients and associated p-values from permutation tests of the associations between *O. europaea* life-stage abundances and NMDS axes. Figures in bold are statistically significant at $p < 0.05$.

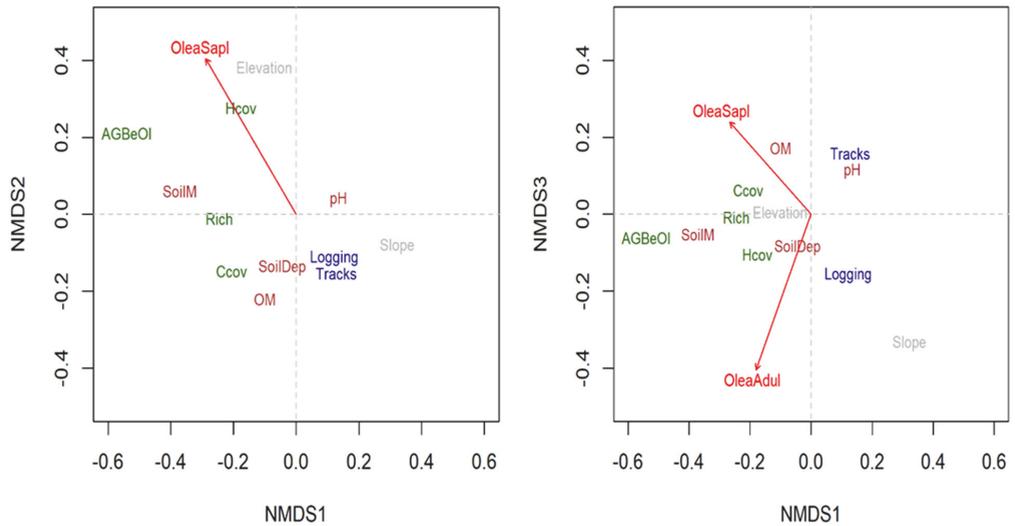| Environmental Variables	NMDS 1 vs NMDS 2		NMDS 1 vs NMDS 3	
	r^2	p	r^2	p
Seedlings	0.0152	0.659	0.0122	0.694
Saplings	0.1997	**0.005**	0.1180	**0.023**
Adult	0.0557	0.205	0.1778	**0.007**

Fig. 3. Nonmetric multidimensional scaling (NMDS) ordination of *O. europaea* life stages versus environmental factors. *O. europaea* life stages in red, topographic factors are shown in dark grey, soil factors in brown, biotic factors in dark green and disturbance factors in dark blue. *O. europaea* adult (OleaAdul), *O. europaea* sapling (OleaSapl), organic matter (OM), canopy cover (Ccov), richness (Rich), track length (Tracks), elevation (Elevation), slope (Slope), number of *O. europaea* stumps (Logging), herbaceous cover (Hcov), aboveground biomass of all trees except *O. europaea* (AGBeOl), soil moisture (SoilM), soil depth (SoilDep) and human footpaths (Tracks).

Woody species richness, aboveground biomass, soil depth, soil moisture, elevation, slope and logging were those variables significantly associated ($p < 0.05$) with the probability of finding *O. europaea* for at least one of its ontogenetic stages. These interactions, revealed by the GLM, indicated ontogenetic niche shifts (Table 2). The probability of finding *O. europaea* increased with higher woody species richness for saplings and adults but decreased for seedlings (Table 2, Fig. 4a). The probability of finding *O. europaea* seedlings increased with soil depth, whereas for saplings it decreased (Table 2, Fig. 4b). The pattern for slope was

similar (Table 2, Fig. 4c). The probability of finding *O. europaea* at all ontogenetic stages increased with logging, but more so for adults and saplings than for seedlings (Table 2, Fig. 4d).

Thus, among the explanatory variables included in both the NMDS and the full GLM model, woody species richness, soil depth, slope and logging had significant two-way interactions with the ontogenetic stages. The negative relationship between slope and the probability of finding saplings, as revealed by the GLM, is reflected also in the ordination diagrams in Fig. 3. In contrast, for the variables woody species richness, soil depth and logging, the interpretation of the NMDS ordination diagrams and the results from the GLM did not correspond.

Table 2. Results of a logistic regression model, estimating how the probability of finding *O. europaea* depends on ontogenetic stage (adults [reference level], sapling, seedling) and environmental factors in Hugumburda dry Afromontane forest in northern Ethiopia. The table shows parameter estimates and associated standard errors for a binary generalized linear model, where the response had two possible outcomes Y (empirical observation) =1 and Y (simulated observation) = 0. Simulated observations were generated by random relocations of the empirical observations of *O. europaea* in 70 sample plots. Figures in bold are statistically significant at $P < 0.05$.

	Estimate	SE	z	p
Intercept	-0.136	0.07	-2.1	**0.037**
Sapling	-0.139	0.12	-1.0	0.317
Seedling	0.275	0.45	0.6	0.542
Richness	0.269	0.08	3.2	**0.001**
Soil depth	-0.051	0.09	-0.6	0.554
Elevation	0.213	0.07	3.1	**0.002**
Slope	0.217	0.07	3.2	**0.001**

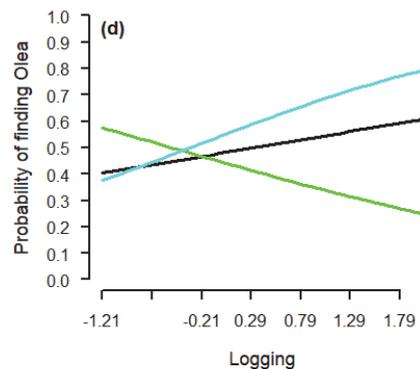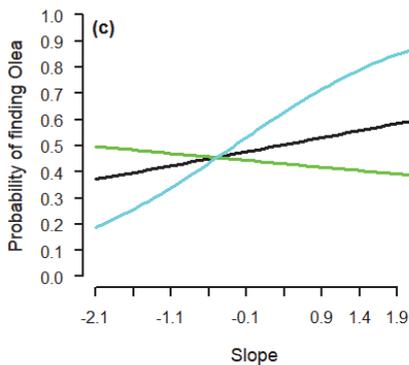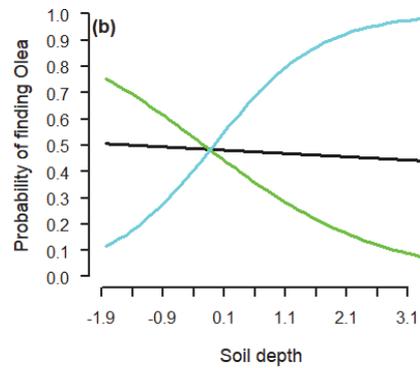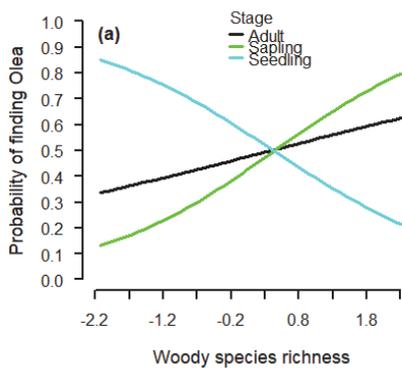|				
Logging	0.253	0.08	3.3	**0.001**
Seedling: Woody species richness	-0.958	0.61	-1.6	0.114
Sapling: Woody species richness	0.467	0.17	2.8	**0.006**
Seedling : Soil depth	1.207	0.57	2.1	**0.035**
Sapling: Soil depth	-0.646	0.17	-3.8	<**0.001**
Seedling : Slope	0.580	0.45	1.3	0.201
Sapling : Slope	-0.324	0.13	-2.4	**0.014**
Seedling : Logging	0.321	0.56	0.6	0.566
Sapling : Logging	-0.687	0.19	-3.6	<**0.001**

Fig. 4. Estimated relationships between the probability of finding *O. europaea* and woody species richness, soil depth, slope and logging, for different ontogenetic stages (adult, sapling, seedling; see Table 2). Note that the explanatory variables were standardized before analysis and plotting. Observed values ranged from 6 to 24 species for woody species richness, from 0.01 to 1.20 meters for soil depth, from 0.03 to 0.94 degrees for slopes, and from 0 to 13 for number of stumps per 20 × 20 m observation plots for logging.

DISCUSSION

This study reveals the presence of ontogenetic niche shifts in *O. europaea*. The probabilities of finding the various life stages related differently to the suites of biotic, abiotic and human disturbance factors that we studied. This suggests that each life stage has a different tolerance to various environmental factors, suggesting niche differentiations in *O. europaea*, as has been found in another threatened tree species, *Acer opalus* ssp. *granatense* (Quero et al., 2008).

The higher probability of finding *O. europaea* seedlings with increasing soil depth suggests that deeper soil is important for seedlings to establish, perhaps because deeper soils retain more soil moisture. Soil depth has been shown to be is an important factor in the establishment of seedlings in recently abandoned pastures and secondary forest in Costa Rica (Gerhardt, 1993). Moreover, in a seed dispersal and establishment experiment on *Olea europaea* in Spain, soil moisture was shown to be the primary determinant of seedling establishment, among several abiotic factors studied (Rey & Alcántara, 2000). Bekele (2005), studying regeneration in a dry Afromontane forest, recorded a higher recruitment rate of *O. europaea* seedlings during the wet seasons than in the long dry season, emphasising the importance of soil moisture in this process.

In contrast, we observed that the probability of finding *O. europaea* saplings decreased as soil depth increased. Because harvesting takes place predominantly at lower elevations, the abundance of both saplings and adults is greater at higher elevations, where the soil is also shallower (Wegasie et al., 2018). This suggests that seedlings may require a different soil moisture regime to that of these later life stages.

The probability of finding sapling and adult *O. europaea* increased with increasing woody species richness. One reason could be that a diversity of other woody plants may create more favourable environmental conditions, thereby enhancing the abundance of saplings and adults (Maestre, Quero, Gotelli, et al., 2012; Wegasie et al., 2018). Such facilitation by woody species has been found previously in dry Afromontane forest in Ethiopia, where the survival of *O. europaea* seedlings was enhanced under shrubs such as *Euclea racemosa*, which effectively served as nurse plants (Aerts, Negussie, Maes, November, Hermy, & Muys, 2007). Shrubs not only assist the establishment of the seedlings but also their long-time survival (e.g. *Acer opalus* subsp. *granatense*: Gómez-Aparicio, Zamora & Gómez, 2005). In our study, however, the probability of finding *O. europaea* seedlings at sites with higher woody species richness was substantially less than that of saplings and adults, perhaps because seedlings experienced competition from established plants.

The higher probability of finding *O. europaea* adults with increasing slope could suggest that it is more difficult to harvest *O. europaea* on steeper slopes (Wegasie et al., 2018). The positive relationship between the probability of finding *O. europaea* adults and logging in the forest is in line with a previous study, which suggested that logging occurs primarily in forest areas dominated by *O. europaea*.

The present population structure of *O. europaea* in Hugumburda reveals a much lower density of seedlings than of saplings and adults. This points to low regeneration of *O. europaea* in the forest compared with other Afromontane forests in the region. For instance, *O. europaea* seedling density in protected parts of Dessea forest was 3113 ± 19 individuals ha^{-1} (Aynekulu, Denich & Tsegaye, 2009), which is much greater than that in Hugumburda (7 ± 5 individuals ha^{-1}). The reason for this low regeneration could be excessive browsing of seedlings by livestock in the forest. Goats *Capra hircus* are the main browsers of *O. europaea* seedlings in dry forest in Ethiopia (Aerts et al., 2007), and we often observed them browsing in the forest during our fieldwork.

The sharp declining in the larger diameter classes could be due to selective logging of big trees in the forest. A similar trend in other montane tree species was observed in Harenna forest, southeastern Ethiopia (Tesfaye, Teketay & Fetene, 2002).

Our findings suggest that there are ontogenetic niche shifts in *O. europaea* in the Hugumburda forest. Seedlings, saplings and adults responded differently to some of the measured environmental and human disturbance variables. In particular, the environmental factors that define the niche of adult *O. europaea* differ from those variables defining the niches of seedlings and saplings. The changes in niche space among these developmental stages reflect ontogenetic niche shifts. Our novel approach of testing our empirical data with simulated data could advance the study of ontogenetic niche shift in plant populations. Finally, because low regeneration rates and moisture stress appear to be the main constraints on *O. europaea* establishment, special attention should be given to protecting seedlings from browsing in an effort to conserve the declining population of *O. europaea* in Hugumburda.

ACKNOWLEDGMENTS

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Paper III

The relationship between reproductive success of a locally endangered tree species, *Olea europaea* subsp. *cuspidata* and human disturbance in an isolated Afromontane forest in Northern Ethiopia

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ABSTRACT

Environmental factors, human disturbance, and individual plant population properties may play a significant role in determining the reproductive success of a plant. Understanding limiting factors for reproduction is important for the conservation of endangered species. We investigated if the reproductive success of a locally endangered tree species, *Olea europaea* subsp. *cuspidata* was related to stem density, individual tree properties, and environmental and human disturbance factors in the isolated dry Afromontane forest, Hugumburda, in Northern Ethiopia. We measured reproductive success (number of flowers, premature fruits, mature fruits), stem density, and individual properties (crown diameter, DBH, height) of *O. europaea* trees, abiotic (soil moisture, soil depth, slope, elevation) and human disturbance factors (track length, logging) from 70 plots (20 m × 20 m) across the forest landscape. We carried out hurdle and general linear mixed effect model (GLMM) analyses to examine the relationships. The probability of *O. europaea* flower occurrence was positively related to crown diameter, but negatively with deeper soils. The likelihood of *O. europaea* flowers resulting in mature fruits was negatively related to longer tracks, and the likelihood of premature *O. europaea* fruits developing into mature fruits was negatively related to steeper slopes and longer tracks in the forest. None of the reproductive success parameters were related to stem density. Our results suggest that human disturbance, by people and livestock, influence the reproductive output in *O. europaea*. Restricting the use of these tracks by people and livestock could perhaps improve the reproduction of *O. europaea.* This is, however, not a good solution for the people, so understanding why this disturbance has a negative influence on reproduction is important to enable forest management and ensure reproduction in the long term.

Key words: Dry land forest; Endangered species; Hugumburda forest; Track length; Tree properties

INTRODUCTION

Human disturbance is the main cause of reduced biodiversity in forest ecosystems (Ewers and Didham, 2006, Aynekulu et al., 2016), and can also affect the reproductive success of individual plant species (Pellegrino and Bellusci, 2014, Fernandez et al., 2015, Torimaru et al., 2018). For instance, plant populations that are isolated because of surrounding agricultural fields may decline in density because of pollen limitation (Chen and Zuo, 2018). In addition, the characteristics of the population itself, such as the density and individual properties, may also influence the reproductive output of plant species (Singh et al., 2018). Thus, understanding the relationship between the reproductive success of an endangered species and its individual properties, and environmental and human disturbance factors may contribute to understand why the population is declining (Shao et al., 2008).

The number of flowers and fruits can express the reproductive success of a plant (Shao et al., 2008, Arena et al., 2018). The number of fruits is the basis for seed production, and thus the recruitment of individuals into the population (Lennartsson, 2002). Moreover, knowledge about which factors that influence the reproductive success is important for understanding the population dynamics, and to develop conservation strategies for endangered species.

Populations of some multipurpose tree species in dry Afromontane forests are shown to decline because of human disturbance (Mligo et al., 2011, Aynekulu et al., 2016). *Olea europaea* subsp. *cuspidata* (hereafter *O. europaea*) is one characteristic tree species in these forests (Bekele, 2005), but because of the multipurpose use of the species, such as for farm implements, fuelwood, construction material, and medicine, it is threatened by over-exploitation and considered locally endangered (Viswanathan, 1986, CBD, 2009). However, despite being much needed, knowledge about the reproductive success of *O. euroapea* is very limited although there have been some previous studies on the abundance, seed dispersal and recruitment of this species (Aynekulu et al., 2009, Abiyu et al., 2016, Abiyu et al., 2017, Wegasie et al., 2018). According to Wegasie et al., 2018(unpublished), there are few *O. europaea* seedlings compared to saplings and adults in the dry Afromantane Hugumburda forest. The reason for this may be a low fruit production per flowers. Thus, we hypothesise that human disturbance affect the reproduction success of *O. europaea* in this forest. The main objectives of this study was to examine (a) if there is a relationship between the reproductive success (number of flowers, premature and mature fruits) of *O. europaea* and

abiotic and human disturbance factors, and (b) if the reproductive success in *O. europaea* is related to its individual properties and density.

MATERIALS AND METHODS

Study species

Olea europaea subsp. *cuspidata* (hereafter *O. europaea*) is naturally distributed from eastern to southern Africa. The tree is native to Ethiopia and is abundant between 1250 to 3100 m a.s.l. in dry Afromontane forests. It occurs primarily in arid areas and adult trees are commonly 15 m high but can reach 25 m (Friis, 1992). It is mainly wind pollinated, and the flowers are hermaphrodite with 6-10 mm long petals and has a creamy white color. However, according to unpublished studies, insects also visit *O. europaea* flowers. The mature fruits are fleshy with an oval shape and a diameter of 10 x 8 mm. The fruit color is green before maturing and brownish when matured. The seeds are mainly dispersed by birds (Abiyu et al., 2016).

Data collection

Reproductive parameters of *O. europaea*

Seventy 20 × 20 m plots were placed on forested slopes at elevations of 2233 - 2503 m a.s.l. in the Hugumburda forest. The plots were distributed about 100 m apart along parallel transects placed perpendicular to three local terrain ridges, each transect running from the top to the bottom of the ridge. The distance between neighbouring transects was ca. 150 m (see Wegasie et al., 2018). We established five small 1 × 1 m plots, one placed in the center of each main plot and four at the center of each diagonals running from the center of the main plots to the corner.

In each 20 × 20 m main plot, we selected one *O. europaea* tree at the centre or near to the centre (66 trees, in total). Among the 70 sample plots, four plots were without *O. europaea* and they were not replaced. For the selected *O. europaea* trees, we measured stem diameter at breast height (DBH), crown diameter (by taking the average horizontal width of the crown) and height (by climbing the trees and using measuring tape).

In each of the selected *O. europaea* trees, ten branches were chosen randomly and marked at 25 cm from the tip to the middle. The sampled trees were monitored three times until fruit maturation. First, the number of flowers on the marked branches were counted during the flowering period (June 2015). All marked branches were revisited for a second

time (September 2015) to count the number of pre-matured fruits. We counted premature fruits to avoid data loss during the fruit maturation period, as ripening fruits are commonly eaten by birds (Abiyu et al., 2016). Finally, we counted the number of mature fruits and removed fruits per branch in November 2015.

We sampled individual properties of *O. europaea* trees, and environmental (topography and soil) and human disturbance variables (track length and number of stumps) in the same plots as we obtained the individual *O. europaea* tree data. We estimated stem density by counting all reproductive *O. europaea* individuals in each plot. The topographic factors, slope and elevation were measured in the center of each main plot with a clinometer and a handheld GPS, respectively. For each main plot, two separate soil samples were collected; the first for soil moisture analysis (collected by soil core samplers at the center of the main plot), and the second for organic content and pH, which was a composite of five samples (top soil to 15 cm depth) collected at the center of each 1 × 1 m plot. The soil samples were sealed in a double plastic bag to preserve the soil moisture. In addition, soil depth was measured in the field by digging a pit at the center of the main plot down to bedrock. All soil samples were transported to Mekelle Agricultural Research Center laboratory in Mekelle. Soil moisture was measured gravimetrically (Black et al., 1965). The composite soil samples were then air-dried at a room temperature and sieved through a 2-mm mesh. Soil pH (at 1:2.5 soil/H_2O) and soil organic matter (Walkley-Black method) were measured using standard techniques (Nelson and Sommers, 1996).
To quantify human disturbance factors, we used a measuring tape to measure the total length (m) of human and livestock footpaths (hereafter tracks) and counted the number of cut *O. europaea* stumps to quantify logging (hereafter logging) in each main plot.

Data analysis

The dataset was subjected to initial exploratory analyses following Zuur et al. (2010) to check for outliers and collinearity between candidate explanatory variables and to explore relationships between number of flowers, premature fruits and mature fruits, and the candidate explanatory variables. We used the statistical software R (R Core Team, 2016) for all exploratory and statistical analyses.

The candidate explanatory variables included individual tree properties (crown diameter, diameter at breast height (DBH) and tree height), soil variables (soil depth, organic

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matter, soil moisture), human disturbance (track length, logging), other abiotic environmental variables (elevation, slope) and stem density of adult *O. europaea* trees in the 20 × 20 m plots. No extreme outliers were detected.

For analyses of factors influencing number of flowers, we carried out a pre-selection of variables, fitting single-variable models for the relationship between number of flowers and each of the candidate explanatory variables, except for DBH and tree height. Because, both these variables were strongly correlated (r≥0.7) with crown diameter. Crown diameter had a stronger statistical signal on the number of flowers; therefore, we used crown diameter as explanatory variable in the statistical modelling. All the candidate explanatory variables that were significantly related to the response (i.e., number of flowers), or suggested a trend (i.e., P<0.10) in the single-variable models, were included in the full (most complex) model. We fitted generalized linear mixed models (GLMMs) with log link function and negative binomial error distribution. An observation-level random intercept was included in the models to deal with over-dispersion. We carried out model selection by backward elimination (Crawley, 2013, Zuur et al., 2013). Explanatory variables were retained in the final model if their influence on the response was statistically significant (P < 0.05) or showed a trend (P < 0.10). For the GLMM models, we used the glmer function through lme4 package in R.

We recognize that using 'number of flowers' a pure count response variable may not be optimal for our dataset, because it included many trees without any flowers. Therefore, we re-fitted the final GLMM model with a hurdle model. The underlying idea for the hurdle model is that there are two ecological processes playing a role. In the context of the *O. europaea* flowers data, one process is causing the absence and presence of flowering, and in those trees that flower, there is a second process influencing the abundance (number) of flowers. The probability function of the hurdle model is build up accordingly. The binomial distribution is used to model the absence and presence of flowers, and a negative binomial (not Poisson, because of over-dispersion in the count data) for the counts (number of flowers). For the hurdle model, we used the hurdle function from pscl package in R. Only the results from the hurdle model is reported in this paper. However, the explanatory variables in the final models were the same for the two modelling approaches, as was the directions of the significant relationships.

Because the fruits develop from the flowers, the number of pre-mature and mature fruits will – to a large extent – depend on the same factors, which influence the number of flowers. Thus, we do not report the results from analyses of factors that influence the number of premature and mature fruits. However, irrespective of whether flowering – and the number of flowers – were related to the human disturbance factors, we wanted to investigate whether the proportion of the flowers that reached the premature or mature stage was influenced by the human disturbance factors.

To analyze if human disturbance influence (A) the probability that *O. europaea* flowers result in mature fruits and (B) the probability that premature *O. europaea* fruits result in mature fruits, we initially fitted GLMMs with a binary response; $Y = 1$ = success (mature fruit) or $Y = 0$ = failure (flower or premature fruit did not results in mature fruit). We used the logit link, assuming binomial distribution of errors. An observation-level random intercept was included in the models to deal with over-dispersion. We included track length, logging (number of stumps) and slope as explanatory variables in the full model. We included slope as explanatory variable in the full models because it may be an indirect measure of accessibility. Explanatory variables were retained in the final model if their influence on the response was statistically significant ($P < 0.05$) or showed a trend ($P < 0.10$).

RESULTS

Among the 70 trees included in the study, 30 trees had flowers (range 1-1225 flowers) on the branch that was selected for flower counts, whereas 40 trees had no flowers on the selected branches. The total number of *O. europaea* flowers (9999) was higher than the total number of premature (2438) and mature (486) fruits. Out of the total number of flowers counted, 24% set premature fruits, but only 5% resulted in mature fruits. Out of the total premature fruits, 20% developed into mature fruits.

The probability that *O. europaea* trees had flowers increased with crown diameter and decreased with soil depth (Table 1A, Figure 1), but these variables were not significantly associated with the number of flowers on trees with flowers (Table 1B). We found no significant association between the probability that *O. europaea* trees – or the number of flowers on flowering trees – and any of the other soil variables (organic matter, moisture), human disturbance (track length, logging), or other abiotic or biotic environmental variables (elevation, stem density of *O. europaea*) (results not reported).

Table 1. Factors influencing flowering in O. europaea in Hugumburda dry Afromontane forest in northern Ethiopia. Parameter estimates and associated standard errors from a hurdle model. The binomial distribution was used to model the absence and presence of flowers (A), and a negative binomial model for the counts (number of flowers). Data from 70 trees (plots) were included in the analysis.

A. Zero hurdle model coefficients (binomial with logit link):

	Estimate	SE	Z	P
Intercept	-0.345	0.280	-1.230	0.22
Crown diameter	1.071	0.337	3.178	0.0015
Soil depth	-0.663	0.324	-2.043	0.041

B. Count model coefficients (truncated negative binomial with log link):

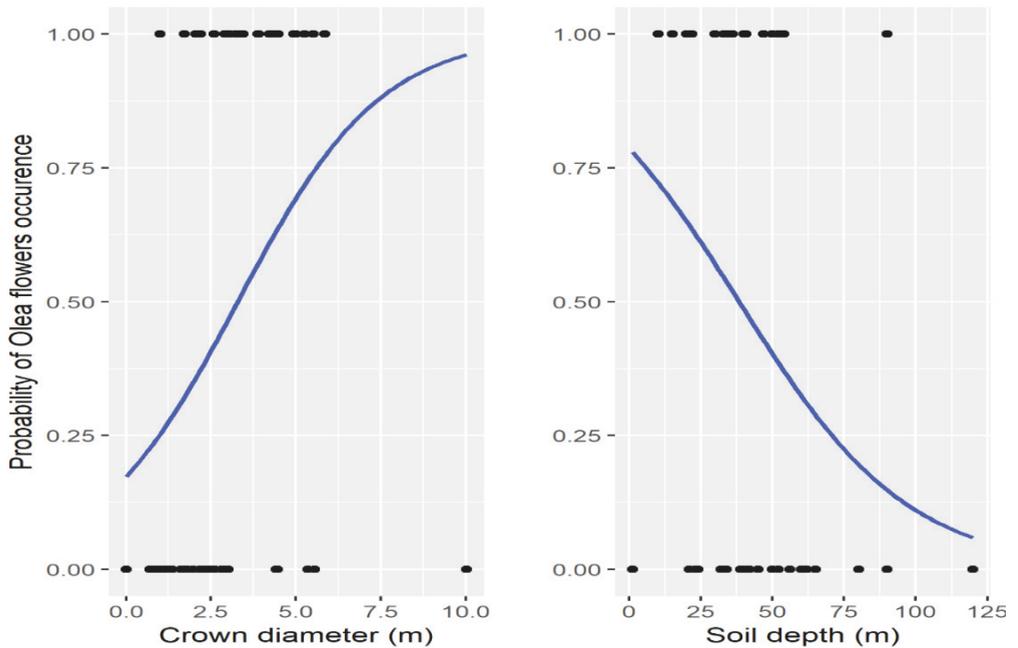|	Estimate	SE	Z	P
Intercept	5.775	0.247	23.405	<0.0001
Crown diameter	0.053	0.338	0.158	0.87
Soil depth	0.118	0.259	0.457	0.65

Figure 1. Estimated relationships between the probability of *O. europaea* flowering and crown diameter (left panel) and soil depth (right panel) in Hugumburda. Figures are based on parameter estimates from the model in Table 1, after removal of the non-significant variables in the count model (B in Table 1). Solid points show observed values.

The probability of *O. europaea* flowers resulting in mature fruits decreased with track length (Table 2A, Figure 2), but was not significantly related to logging (z = 0.02, p = 0.98) or slope (z = -0.85, p = 0.39). Only 8 of the 66 trees included in the analyses had mature fruits (4 trees were excluded because of missing data). The number of removed fruits were recorded for all trees (see methods), but not included in the response variable. When calculated as a percentage of the observed mature versus removed fruits, 78% mature fruits were removed. The probability that premature *O. europaea* fruits resulted in mature fruits decreased with both track length and slope (Table 2B, Figure 3), but was not significantly related to logging (z = -1.06, p = 0.29).

Table 2. (A) Factors influencing the probability that *O. europaea* flowers result in mature fruits. (B). Factors influencing the probability that premature *O. europaea* fruits result in mature fruits. Parameter estimates and associated standard errors are from generalized linear mixed models with logit link function and binomial error distribution. An observation-level

random intercept was included in the models to deal with over-dispersion. Data from 66 trees (plots) were included in the analysis (4 of the trees in Table 1 were excluded because of missing data)

A. Probability of *O. europaea* flowers result in mature fruits

	Estimate	SE	Z	P
Intercept	-3.84	1.096	-3.51	0.00046
Track length	-1.62	0.777	-2.08	0.037

B. Probability that *O. europaea* premature fruits result in mature fruits

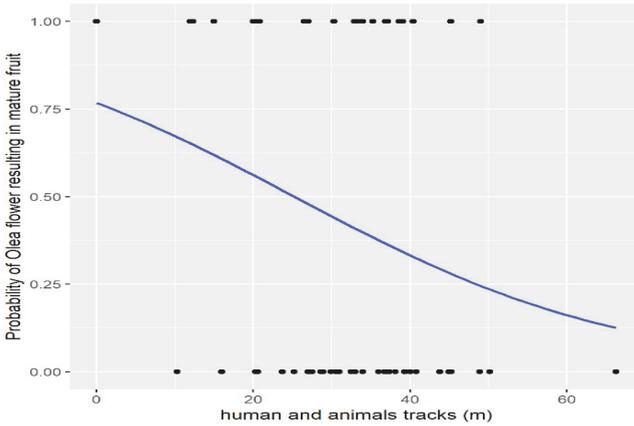|	Estimate	SE	Z	P
Intercept	-9.101	1.831	-4.97	<0.0001
Track length	-1.834	0.994	-1.85	0.065
Slope	-1.925	0.966	-1.99	0.046

Figure 2 . Estimated probability that *O. europaea* flowers result in mature fruits, as a function of track length (human and animals tracks) in the Hugumburda forest. The estimated relationship is based on the model in Table 2A.
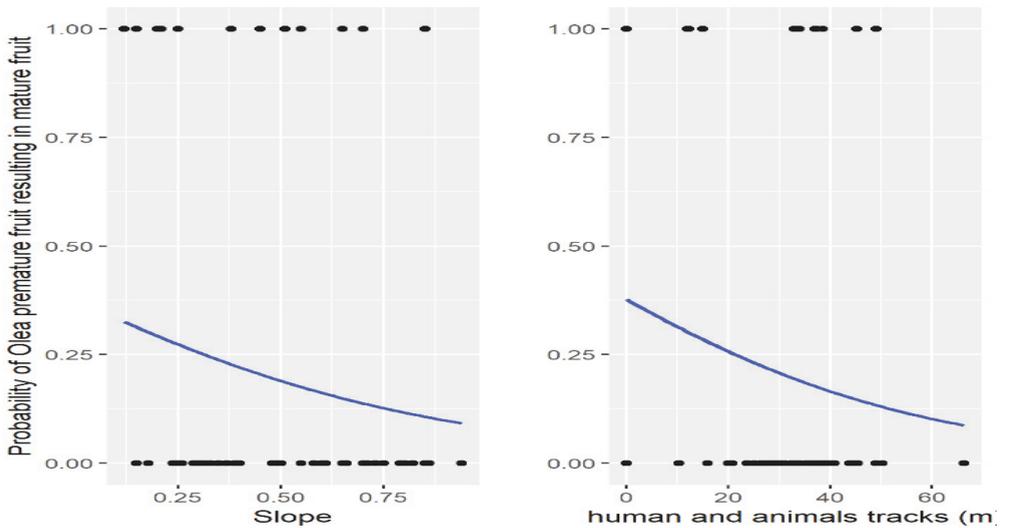

Figure 3. Estimated probability that premature *O. europaea* fruits result in mature fruits, as a function of track length (human and animals tracks) and slope in the Hugumburda forest. The estimated relationship is based on the model in Table 2B.

DISCUSSION

       Our study of the reproduction of *O. europaea* shows that very few flowers developed into mature fruits in the dry Afromontane Hugumburda forest. We found that the probability of flowering was related to individual tree properties and environmental conditions, but it was not related to human disturbance factors. In contrast, the probability that flowers developed into premature and mature fruits was negatively related to human disturbance factors and environmental conditions, but not to individual tree properties.

       We observed significant relationships between the probability of reproductive success in *O. europaea* and canopy diameter, soil depth, slope and human disturbance (length of tracks). Whereas there was no relationship between the density of *O. europaea* stems and the reproductive success. The positive relationship between the probability of *O. europaea* flower occurrence and canopy diameter suggests that trees with wider crown diameter produce more flowers and fruits than trees with smaller canopies. Crown diameter was positively correlated with tree height in our study; this shows that bigger trees with more biomass produce more flowers, which is in line with previous studies (Sanni et al., 2018). Wider canopies are also shown to facilitate flowering in day-neutral strawberry in Korea (Fridiaa et al., 2016). On the other side, denser canopies may create shadow, and thus limit flower production for light demanding plants. Nevertheless, *O. europaea* is shade tolerant tree species for thus canopy shade may not affect its flowering. In our study, we found the probability of *O. europaea* flower occurrence decreased with deeper soils. The reason for this could be stem density might be affected with soil depth (Slik et al., 2010). Moreover, at deeper soil there might be low stem density with deeper soils because of high vegetation diversity that promotes competition among plant species (Loumou and Giourga, 2003), and as a result, the canopy be closed that limit sunlight and flower production.

       The probability of *O. europaea* flowers and premature fruit resulting in mature fruits decreased with longer tracks in the forest. This suggests that areas in the forest that are visited more frequently have lower number of fruits. This can be because people and animals using the tracks might harvest the fruits. Another explanation can be that high disturbance by people and their livestock might create gaps in the forest, and hinder the trees to cross-pollinate with neighboring conspecific trees (Pellegrino and Bellusci, 2014), which result in influencing fruit production. On the other hand, there was no relationship between *O. europaea* tree density and any of the reproductive success in our study. Human disturbance has been shown to decrease pollinator attraction and increase inbreeding, and

thus decrease the fruit production in *Mediterranean orchids* (Pellegrino and Bellusci, 2014). In addition to human disturbance, the reason for low fruit production may be due to flies feeding on *O. europaea* fruits (Mkize et al., 2008), which could lead to abscission of fruits (Stephenson, 1981). The probability of premature fruits developing into mature fruit decreased with steeper slopes in our study. According to (Wegasie et al., 2018), adult *O. europaea* trees are dominated at higher elevation which is steep slope. However, in case of *O. europaea* there, fruit predators e.g. monkey and birds might access the fruits because as they can climb and frequently visit fleshy *O. europaea* fruits for food (Mokotjomela et al., 2013, Abiyu et al., 2017). This might show that the high harvesting of *O. europaea* fruits on steep slopes, which influence the probability of premature fruits resulting in mature.

Our study of the reproductive success of *O. europaea* suggests that human disturbance has a negative influence on both the production of premature fruits, and on the development from premature to mature fruits. For the management and conservation of the species, tracks length could be considered to reduce the disturbance by restrict people to only use a few tracks. However, we need better understanding of why human disturbance is negatively related to the reproductive success of *O. europaea*, so more studies are needed on the mechanisms behind this relationship, such as for example if there is pollen limitation in *O. europaea*.

ACKNOWLEDGMENT

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Paper IV

Illegal Harvesting of Locally Endangered *Olea europaea* Subsp. *cuspidata* (Wall. ex G. Don) Cif. and Its Causes in Hugumburda Forest, Northern Ethiopia

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Abstract: *Olea europaea* L. subsp *cuspidata* (Wall. ex G. Don) Cif., an endangered tree species in dry Afromontane forests, has multiple uses in local communities in Ethiopia, making it susceptible to overexploitation. The study investigated the rates and causes of *O. europaea* harvesting in the Hugumburda National Forest Priority Area (NFPA). We measured the diameter at stump height of harvested stumps from 70 (20 × 20 m) plots and estimated the time since cutting to determine the biomass of *O. europaea* wood harvested annually in the forest. We performed a socioeconomic survey of the reasons for wood harvesting by conducting 163 stratified random individual interviews in the villages surrounding the forest. The average annual quantity of *O. europaea* wood illegally harvested from the forest was estimated to be 430 kg ha^{-1}, mainly for farm implements, fuel wood, and fumigation purposes. The results of a General Linear Model (GLM) show that the extraction of *O. europaea* wood in the forest is higher at higher elevations than at lower, and the number of *O. europaea* stumps in the forest is higher at an intermediate distance to the villages. We show that *O. europaea* is harvested in the forest despite the fact that the forest is protected. Permanent sample plots should be established to monitor the increment.

Keywords: African olive; dry Afromontane forest; fuel wood; farming implements; multipurpose tree; socioeconomic survey

1. Introduction

Dry Afromontane forests are dominant in Ethiopian highlands [1,2]. The highlands cover more than 50% of the country's total area, and common practices there are crop production and livestock rearing [2,3]. Illegal logging and agricultural land expansion towards the forest edge are the main factors contributing to forest degradation [4–6]. The energy demands of the increasing population are mainly supported by biomass [7,8], which is derived from fuel wood, agricultural residues, and cow dung. Most people in the local communities cannot afford alternative energy sources [9], and the low incomes earned by rural families are often inadequate to meet their basic needs. As a result, forests close to the local communities have been affected by illegal logging both for home consumption and as a means of generating income [10]. The illegal harvesting of wood may lead to the destruction of the forests, and therefore the Ethiopian government has declared and implemented policies for managing

58 National Forest Priority Areas (NFPAs), covering 3.6 million ha, with the purpose of maintaining forest genetic resources. However, these policies have not been successful, as wood harvesting has continued to take place in the protected areas [11].

Hugumburda National Forest Priority Area (hereafter Hugumburda forest) has higher plant diversity compared with other forests and NFPAs in northern Ethiopia [12]. *Olea europaea* subsp. *cuspidata* (Wall. ex G. Don) Cif. (hereafter abbreviated as *O. europaea*), commonly known as African olive, is a multipurpose tree species found widely distributed in the forest [11,13]. The wood is used for fuel, fumigation (smoke baths), farm implements, house building and furniture, and the leaves are used for medicine. For example, the unique fragrance from the smoke of burnt *O. europaea* is used as a pleasant scent in homes, for flavoring traditional drinks, and as an insect repellent [14]. Negash [15] states that because of its economic and traditional benefits, the population of *O. europaea* is declining in Ethiopia due to overexploitation and needing in situ conservation at a national level [16–19]. However, there is limited knowledge about the harvesting rate of the species in Hugumburda forest. Accordingly, the main objectives of the study were: (1) to estimate the annual harvest of *O. europaea* in Hugumburda; (2) to identify the pattern in the annual harvesting of the species in relation to distance from the villages, slope, and elevation; and (3) to assess the socioeconomic importance of *O. europaea* for local households.

2. Materials and Methods

2.1. Study Area

Hugumburda National Forest Priority Area (12°36′ N, 39°31′ E) is situated in the southern part of Tigray Region, Ethiopia. The altitudinal range is 1860–2700 m a.s.l. (meters above sea level) [12]. Average daily temperatures are in the range of 14.6–22.4 °C, with a minimum of 8.8 °C in October and a maximum of 34.3 °C in June, and the average annual rainfall is 705–986 mm [13]. The forest was designated as a National Forest Priority Area in 1993 [11].

The forest is located ca. 630 km north of Addis Ababa, the capital of Ethiopia. There are four districts bordering the forest: Alamata, Endamehoni, Ofla, and Raya Azebo. The extraction of any resources within the forest except dead wood and cactus fruit is forbidden by law.

2.2. Data Collection

2.2.1. Ecological Survey

We compiled a forest inventory to enable us to estimate the extent of the harvesting of *O. europaea* in Hugumurda Forest. Initially, a reconnaissance survey was performed to identify *O. europaea*-dominated areas of the forest. Then, 70 sample plots (20 m × 20 m) (Figure 1) were laid out in *O. europaea*-dominated areas in which all *O. europaea* stumps could be counted and their diameter at stump height (DSH) measured, in order to estimate the aboveground biomass of the wood that had been cut and removed from the forest. The plots were marked ca. 100 m apart along parallel transects placed perpendicular to three local terrain ridges, with each transect running from the top to the bottom of the ridge. The distance between neighboring transects was ca. 150 m. The time since harvest (hereafter referred to as stump age) of each stump was estimated by the freshness of exposed wood and coppices, in order to estimate the annual harvest rate. Stumps with freshly exposed wood and without coppices were estimated as one year old. The age of stumps with older exposed wood and small sprouts was estimated as two years old, and those with coppices and signs of decomposition were estimated to be more than two years old. We roughly determined the purpose of illegal harvesting on the basis of the stump diameters (i.e., DSHs). Local farmers and forest guards assisted us with stump age estimation and identification of the reason for cutting. Other information collected from each plot included slope and elevation measured at the center of each main plot with a clinometer and a handheld GPS respectively. By overlaying 70 plots in Google Earth software version 7.2 (Google, California, CA, USA), we were able to measure the distance from each sample plot to the nearest

village, Hugumburda to see how the accessibility related to the harvesting rates. The Hugumburda village was the nearest village to all sample plots.
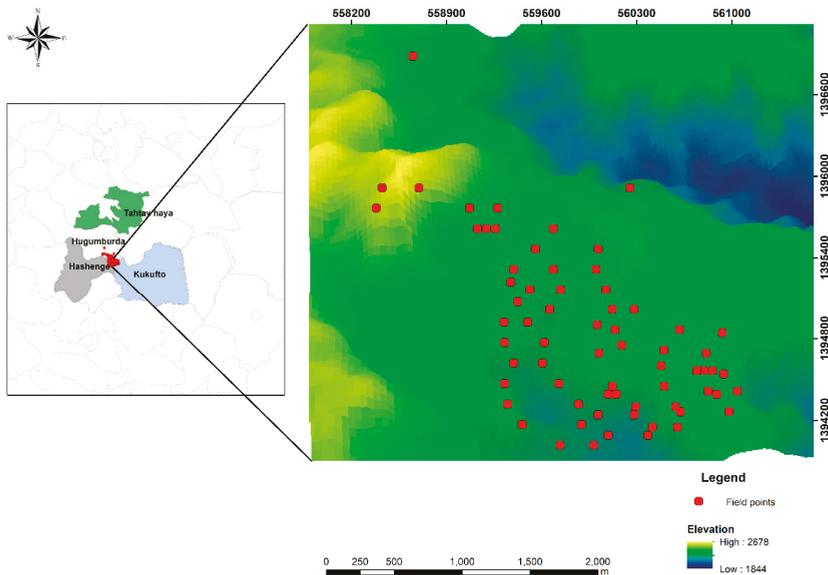

Figure 1. The sample plots in Hugumburda Forest in relation to the study villages, Hashenge, Kukufto, and Tahtay Haya.

2.2.2. Socioeconomic Survey

We conducted a socioeconomic survey in three villages to assess human activities relating to the harvesting of *O. europaea* in the reserve. Three villages, Kukufto, Hashenge, and Tahtay Haya, were selected from the three neighboring districts of Raya Azebo, Ofla, and Endamehoni, respectively, based on their proximity to the forest. In order to avoid sampling bias, we did not conduct a socioeconomic survey in Hugumburda village because some of the households lived within the forest. Representatives of 162 households and 54 respondents from each village were interviewed. Systematic stratified sampling was used to select households, with the aim of including both genders and different economic statuses, age classes, and educational backgrounds. A semi-structured questionnaire was developed and pre-tested twice. The survey was conducted from March to May 2016.

The questionnaire was designed to provide demographic information, such as gender, age, education, profession, job type, economic status, marital status, and different uses of *O. europaea* wood; frequency of using *O. europaea* wood; and places where the household obtained *O. europaea* wood for different purposes. The age of each respondent was classified into one of four age groups: 15–24 years, 25–44 years, 45–64 years, and 65+ years. The data were collected by conducting face-to-face personal interviews in the local language, Tigrigna.

In addition, direct preference ranking was done to identify the local community preference for plant species for fuel wood and traditional toothbrush uses. The names of common plants were listed and the respondents were divided into 16 groups, each with 9–10 respondents, and requested to rank their preferences for fuel wood and cleaning teeth use. After the ranking was completed, the scores for each species were counted and the preference list was compiled on the basis of the highest score.

Additionally, a fuel wood market survey was conducted to quantify the amount of *O. europaea* wood products being traded at the local markets. In addition, the market price for the same products

in Mekelle, the capital of Tigray, was assessed for comparison. During the survey, 12 *O. europaea* wood sellers were found in two marketplaces, Shoko Majo and Kukufto, located in Endamehoni and Raya Azebo districts, respectively. Each marketplace was represented by six wood sellers and they were interviewed about the quantity of *O. europaea* wood and the price at the local market. In addition, the same fuel wood survey was conducted to five marketplaces (Aider, Adiha, Adihawsi, Lachi, and Ashirte shewuate) in Mekelle town. Seven *O. europaea* wood merchants from each of the markets, 35 in total, were interviewed. The amount of *O. europaea* wood traded in the fuel markets was quantified by weighing each bundle and converting the local unit of measurement (bundle of wood) into kilograms.

2.3. Data Analysis

2.3.1. Data Preparation

To determine the quantity of *O. europaea* wood harvested annually (hereafter called the harvesting rate), we summed the aboveground biomass of all *O. europaea* trees cut during the last year (i.e., stumps classified as one year old). The sum of individual tree aboveground biomass was divided by 0.04 to find the harvested biomass in kg ha^{-1} year^{-1} for each sample plot, since all sample plots were 400 m^2.

The aboveground biomass (AGB) of *O. europaea* wood harvested in Hugumburda forest was calculated using the allometric equation developed by Parent [20] for oven-dry biomass of *O. europaea* trees in Ethiopia:

$$\text{AGB (in kg)} = (0.6806 \times \text{DSH}) + (0.0422 \times (\text{DSH}^{2.7})), \tag{1}$$

where AGB = aboveground biomass of individual *O. europaea* tree (kg) and DSH = the diameter at stump height (cm). The estimated biomass did not include roots and foliage.

2.3.2. Statistical Analysis

The ecological dataset was first subjected to exploratory analyses following Zuur et al. [21], to check for outliers and collinearity between candidate explanatory variables and to explore the relationships between the response and candidate explanatory variables. To avoid collinearity, we made a correlation matrix with correlation coefficients (r) for all possible pairs of candidate explanatory variables. Pearson correlation coefficients test were used for the continuous explanatory variables.

We used two different estimates of harvested amount (number of stumps and harvesting rate) because they were not strongly correlated (Pearson correlation: $r = 0.53$, $p < 0.001$. This is not so surprising, given that the diameter distribution of harvested *O. europaea* trees was quite variable. This means that for example 10 random samples of 10 harvested trees, would have a high among-samples variation in biomass. The two different estimates of harvested amount were influenced by different explanatory variables. By using only one of them, we would miss interesting patterns of association with the explanatory variables. Therefore, we chose to use both of them.

To determine whether there was a relationship between the harvesting rate of *O. europaea* (i.e., the quantity of *O. europaea* wood harvested from the forest annually) and the explanatory variables, we fitted a general linear model (GLM) with an identity link function, assuming a Gaussian distribution of errors. Explanatory variables included in the full model were elevation, slope, distance to nearest village, and the second power of each of these variables, to capture "humped-backed" relationships detected in the exploratory analyses.

To determine whether there was a relationship between the number of harvested stumps of *O. europaea* and the explanatory variables, we fitted a generalized linear model (GLM) with log link function, assuming a Poisson distribution of errors. However, this model was overdispersed (generalized Pearson statistic (gPs) = 4.01); therefore, we refitted the model with a negative binomial GLM (gPs = 0.99). Explanatory variables included in the full model were elevation, slope, distance to nearest village, and the second power of each of these variables, to capture "humped-back" relationships detected in the exploratory analyses.

Initially, we did not consider number of stumps as a response variable because harvesting rate was calculated from the number of stumps. However, during data exploration, we found that number of stumps had a strong relationship with distance from the nearest village but harvesting rate did not have a similarly strong relationship. Therefore, we performed separate analyses for the two variables, assuming both variables as a response variable, to determine how harvesting rate and number of *O. europaea* stumps were related to slope, elevation, and distance to nearest village.

To determine whether the probability that a household harvested *O. europaea* wood directly from the forest ("yes" or "no") was influenced by the candidate explanatory variables sampled in the socioeconomic surveys (Table 1), we fitted a GLM, assuming a binomial distribution of errors and using the logit link function. Many of the candidate explanatory variables were strongly correlated (i.e., collinearity problem) and not significant to the response variable during the single variable model selection. Therefore, only explanatory variables that had a statistically significant influence ($p < 0.05$) on the response in the single variable models were included as explanatory variables in the full model. Among the candidate explanatory variables described in Table 1, only the variables "Use of *O. europaea* wood for fuel wood," "Villages," "Household head," and "Frequency of use of *O. europaea* wood for fumigating the home" were included as explanatory variables in the full model, with "Likelihood of harvesting *O. europaea* from Hugumburda forest" as a response variable. The other candidate variables were not included in the full model, either because they had no significant influence on the response variable in single-variable models ($p > 0.05$), or because they were strongly correlated ($r > 0.7$) with one or more of the explanatory variables (indicated in bold in Table 1). Polychoric correlation tests [22], i.e., tests of association between ordinal variables, were used to identify correlations between candidate categorical explanatory variables in the socioeconomic dataset: village; age class; family size; education level; household head; marital status; economic status; places to collect *O. europaea* wood for fuel wood, fumigation, and farm implements; use of *O. europaea* wood for fuel wood, fumigation, and farm implements; frequency of use of *O. europaea* wood for fumigation; and whether or not *O. europaea* trees were planted in the backyard (Table 1). In cases of correlation ($r > 0.7$) between two candidate variables, we selected the variable most strongly correlated with the response (i.e., the highest *r*-value) for inclusion in the full (most complex model), while at the same time avoiding collinearity with other variables.

Table 1. Description of response and candidate explanatory variables used in the model within the socioeconomic dataset. Only explanatory variables in bold were included in the full model explaining the Likelihood of harvesting *Olea europaea* (Wall. ex G. Don) Cif. from Hugumburda Forest. The other variables were not included in the full model, either because they had no significant influence on the response variable or because they were strongly correlated ($r > 0.7$) with one or more of the variables in bold.

Variables	Description
Response Variable	
Likelihood of harvesting *O. europaea* from Hugumburda Forest	The probability that a household harvested *O. europaea* wood directly from the forest (yes or no)
Candidate explanatory variables:	
Villages	Hashenge, Kukufto, and Tahtay Haya (administrative units)
Age class	Age of the household head in years (15–24, 25–44, 45–64, or 64 +)
Family size	Number of family members
Education level	Number of school years completed by the household head (0, 1–5, 6–10, 11–12, or 12 +)
Household head	Male-headed or female-headed household
Marital status	Household situation with regard to whether household head is single, married, separated, divorced, or widowed
Economic status	Whether the household is poor, middle-income, or rich
Use of *O. europaea* wood for fuel wood	A household using *O. europaea* wood for fuel wood (yes or no)
Use of *O. europaea* wood for fumigation	A household using *O. europaea* wood for fumigation (yes or no)
Places obtaining *O. europaea* wood for fumigation	A household obtaining *O. europaea* wood for fumigation (from backyard, market or the forest)

Table 1. *Cont.*

Variables	Description
Response Variable	
Frequency of use of *O. europaea* wood for fumigating the home	The frequency of a household head using *O. europaea* wood to fumigate his or her own house (daily, every three days, once per week, or three times per week)
Use of *O. europaea* wood for farming implements	A household using *O. europaea* wood for farming implements (yes or no)
Places obtaining *O. europaea* wood for making farm implements	A household obtaining *O. europaea* wood for making farming implements (from backyard, market or the forest)
A household head planted *O. europaea* in his/her garden	A household that has planted an *O. europaea* tree (yes or no)

For the generalized linear models, we carried out model selection by stepwise variable selection procedure, which retains or drops explanatory variables to produce a model that minimizes the Akaike information criterion (AIC) using the stepAIC function in the MASS package in R. The model was fitted using the package in R version 3.4.4 software (R Core Team, Vienna, Austria, 2018).

Responses collected during preference ranking were used to identify the plants that were most important for fuel wood and cleaning teeth from the woody species in the forest. The respondents' scores were counted and ranked from the highest to lowest. Descriptive statistical methods were used to summarize the data.

The fuel wood data collected from the market places were used to show the demand for *O. europaea* wood in the rural villages and big town such as Mekelle. Accordingly, the average price was estimated for each *O. europaea* wood bundle weighed from seven local merchants and 35 Mekelle town fuel wood merchants.

3. Results

3.1. Amount of O. europaea Wood Harvested

The stump survey revealed that the average annual *O. europaea* wood harvest rate was 430 kg/ha of the surveyed part of Hugumburda Forest. The 95% confidence interval for this estimate was between 250 kg/ha and 620 kg/ha. Given that the total forested area in the study area was 8103 ha, the total biomass of *O. europaea* wood harvested in the reserve during the study period was probably between 2000 and 5000 tons.

A frequency distribution plot of the diameter classes shows that the frequency of cutting *O. europaea* trees with small diameters (1–4 cm) was higher than for those in the large diameter classes (5–13 cm) (Figure 2). This might have been due to the high abundance of small *O. europaea* trees in Hugumburda forest.
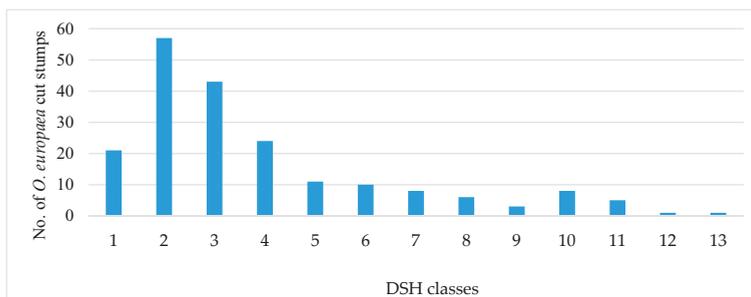

Figure 2. Number of *Olea europaea* (Wall. ex G. Don) Cif. stumps in different diameter classes in Hugumburda Forest. DHS class 1 = 0–2.9 cm; 2 = 3–5.9 cm; 3 = 6–8.9 cm; 4 = 9–11.9 cm; 5 = 12–14.9 cm; 6 = 13–17.9 cm; 7 = 18–20.9 cm; 8 = 21–23.9 cm; 9 = 24–26.9 cm; 10 = 27–29.9 cm; 11 = 30–32.9 cm; 12 = 33–35.9 cm; 13 = 36–38.9 cm.

3.2. Factors Influencing the Amount of O. europaea Harvested

The general linear model explained 11% of the variation in the harvesting rate of *O. europaea* (Table 2). Annual harvesting rate of *O. europaea* was positively related to elevation in the forest (Figure 3). For instance, the annual harvesting rate increased by 100 kg/ha when elevation increased 2300–2400 m a.s.l. This might have been due to the high abundance of *O. europaea* trees at higher altitudes (Table 2 and Figure 3).

Table 2. Factors influencing the harvesting rate of *Olea europaea* (Wall. ex G. Don) Cif. in Hugumburda dry Afromontane forest in northern Ethiopia. Also shown are the parameter estimates (β) and associated standard errors and *t*-values for a linear model of the relationship between *O. europaea* harvesting rate and the explanatory variables retained in the final model ($Y = 0.423 + 0.262x$, $R^2 = 0.11$).

	β	SE	*t*	*p*
Intercept	0.423	0.094	4.480	<0.001
Elevation (m a.s.l.)	0.262	0.095	2.757	<0.001

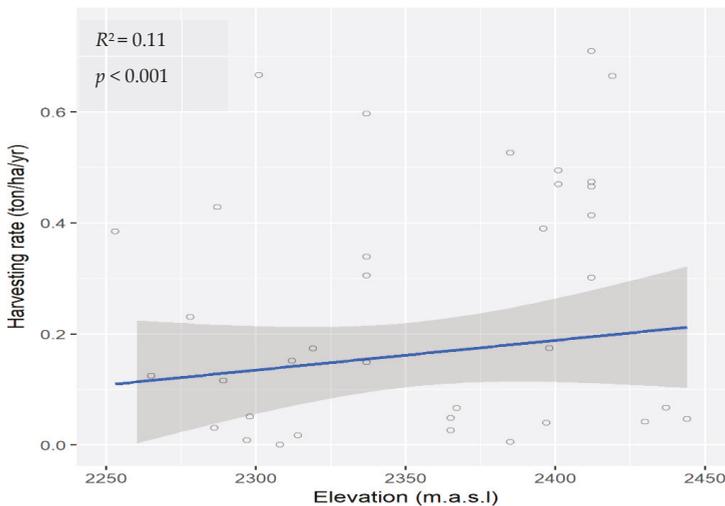m a.s.l., meters above sea level.

Figure 3. The relationship between harvesting rate of *Olea europaea* (Wall. ex G. Don) Cif. and elevation in Hugumburda dry. Afromontane forest in northern Ethiopia. The solid lines indicate the fitted lines and the shaded polygons denote the 95% confidence intervals. The grey circles show observed values. m a.s.l., meters above sea level.

The general linear model explained 17% of the variation in the number of *O. europaea* stumps. There was a "humped-back" relationship between the number of *O. europaea* stumps and distance from the nearest village (Table 3). For instance, the number of stumps increased when the distance from the nearest village increased from 1 km to 2 km. However, the number of stumps showed a decreasing trend when the distance increased from 2.5 km to 4 km (Figure 4).

Table 3. Factors influencing the number of *Olea europaea* (Wall. ex G. Don) Cif. stumps in Hugumburda dry Afromontane forest in northern Ethiopia. Also shown are the parameter estimates (β) and associated standard errors and *z*-values for the relationship between the number of *Olea europaea* stumps and other explanatory variables retained in the final model ($Y = 1.222 + 0.118x - 0.333x^2$, $R^2 = 0.17$).

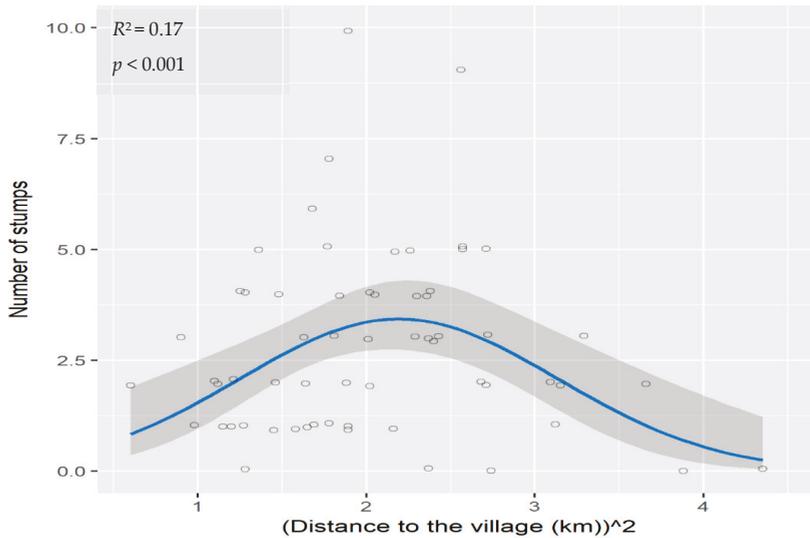|	β	SE	z	p
Intercept	1.222	0.110	11.072	<0.001
Distance from the nearest village (km)	0.118	0.119	0.987	0.324
Distance to the nearest village (km^2)	−0.333	0.100	−3.339	<0.001

Figure 4. The relationship between the number of *Olea europaea* (Wall. ex G. Don) Cif. stumps and distance from the nearest village in Hugumburda dry Afromontane forest in northern Ethiopia. The solid lines indicate the fitted lines and the shaded polygons denote the 95% confidence intervals. The grey circles show observed values.

3.3. Household Consumption of O. europaea Wood

The three case villages represented 54% (Kukufto), 28% (Hashenge) and 18% (Tahtay Haya) of the total number of households (7011) in those villages. The majority of respondents interviewed (96%) in the villages confirmed that fuel wood was their main source of energy (Table 4). According to the preference ranking of plant species, *Cadia purpurea* Willd. and *O. europaea* were the villagers' preference for fuel wood; only 3% of the respondents used cow dung, and only 1% used electricity.

In addition to fuel wood, the preference-ranking analysis was also conducted to rank the most common plant species used for oral hygiene (traditional toothbrush). During the interviews, seven of the most important plant species for fuel wood and six for cleaning teeth use were identified among 40 woody species from the forest. *O. europaea* and *Dodonaea viscosa* (L.f.) Benth. var. *angustifolia* were the main species preferred by the villagers (Table 5).

Table 4. Energy sources and plant species used for cooking (fuel wood) ranked by the respondents' preferences.

Types of Energy	Preferred Species for Fuel Wood	No. of Respondents	Rank
Fuel wood	*Cadia purpurea* Willd.	57	1
	O. europaea (Wall. ex G. Don) Cif.	51	2
	Carissa edulis L.	15	3
	Eucalyptus camaldulensis Dehnh.	9	4
	Dodonaea viscosa (L.f.) Benth. var. angustifolia	5	5
	Juniperus procera Hochst. ex Endl.	1	6
	Clerodendrum villosum De Wild	1	7
	Others	15	–
Cow dung		5	–
Electricity		2	–

Table 5. Respondents' total scores and ranking of the six plant species used for cleaning teeth.

Species Used for Cleaning Teeth	Total Score	Percentage	Rank
O. europaea (Wall. ex G. Don) Cif.	154	92.8	1
Dodonaea viscosa (L.f.) Benth.	57	34.3	2
Pittosporum viridiflorum Sims	15	9.0	3
Cardia purpurea Willd.	11	6.6	4
Euclea racemosa subsp. *schimperi* A.DC. F. White	6	3.6	5
Others	38	22.9	6

3.4. The Main Uses of O. europaea Wood

The majority of respondents indicated that fuel wood, fumigation, and farm implements were the three main uses of *O. europaea* wood. For fuel wood, both the stem (80.7%) and branches (69.2%) were ranked as the main parts of the trees that were preferred and the leaves (3%) were the least preferred part. For fumigation, both the stem (90.3%) and the roots (74.1%) were the main preferred parts and the bark (0%) was not used at all. For making farm implements, branches (77.7%) were ranked as the main preferred part of *O. europaea*, the stem (50%) was the second most preferred part, and the least preferred part were the roots. When we asked respondents whether they used *O. europaea* wood for different purposes, the majority (83%) responded that they used it for fumigation, and almost as many (76%) said they used it for making farm implements.

In the local markets, 1 kg of *O. europaea* wood was sold at a price of 6.56 ± 1.92 Ethiopian Birr (ETB), yet in Mekelle town the price was 3.9 ± 0.51 ETB. The prices were converted from ETB to United States dollars (USD), using an exchange rate of 1 USD to 21.59 ETB (April 2016 exchange rate). Therefore, 100 kg of *O. europaea* wood at the local wood market was estimated as having a value of 30.89 ± 8.91 USD, which was more than the equivalent price per 100 kg at Mekelle town's wood market (17.94 ± 2.38 USD).

Both the geographical location of a household and its use of *O. europaea* for firewood affected the likelihood of the household's members harvesting and collecting *O. europaea* wood directly from the forest (Table 6 and Figure 5). There was a highlight probability of people living in Kukufto harvesting *O. europaea* from the forest compared with people from Tahtay Haya and Hashenge, and people from the Hashenge forest had the lowest probability of harvesting *O. europaea* from the forest. Households that used *O. europaea* for firewood were more likely to obtain the wood directly from the forests than were households that did not use it for firewood.

Table 6. The estimated likelihood *O. europaea* (Wall. ex G. Don) Cif. being harvested from Hugumburda Forest by people from different villages adjacent to the forest, based on results from a binary GLM (response: harvest versus non-harvest) with logit link function. GLM, General Linear Models. Also shown are the parameter estimates (β) and associated standard errors and *z*-values.

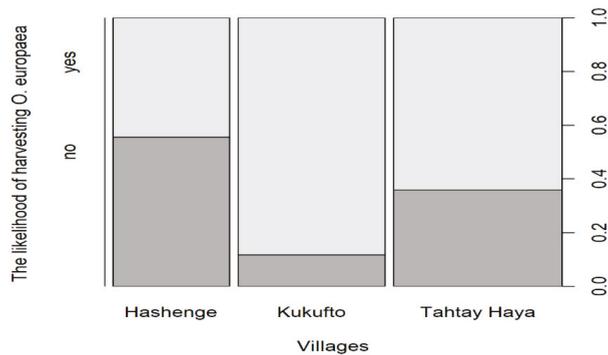|	β	SE	*z*	*P*
Intercept (Hashenge)	−0.223	0.387	−0.576	0.565
Kukufto	2.238	0.658	3.400	0.001
Tahtay Haya	0.803	0.511	1.570	0.116

Figure 5. The likelihood of *O. europaea* (Wall. ex G. Don) Cif. wood being harvested from the forest by the respondents living in the three villages adjacent to Hugumburda forest.

4. Discussion

We estimated that a quantity of 2000–5000 tons of *O. europaea* wood biomass was harvested from 8103 ha of Hugumburda Forest during 2016 (i.e., the study year). Since our sample plots were located in parts of the forest where the species was abundant, the actual removal might have tended towards the lower end of this interval. To our knowledge, no estimates of increment or yield of *O. europaea* in Hugumburda Forest have been made to date. However, the reported mean annual increment (MAI) of *O. europaea* in Desa'a dry Afromontane forest (a similar forest type to Hugumburda Forest, located in same region) is 1.083 m^3 ha^{-1} [23]. If this estimate were applied to the forest area of Hugumburda, the total increment of *O. europaea* would be more than 8700 m^3 per year. Using the basic specific gravity of 0.72 [24], 8700 m^3 is equal to 6300 Mg of biomass. This indicates that removal is below the estimated increment and that the ongoing illegal harvest is not seriously degrading the population of *O. europaea* in the forest. However, this estimate is rather speculative. Based on the interviews, we found that the *O. europaea* wood harvested was used for different purposes, including farm implements, fuel wood, and fumigation. An ethnobotanical study conducted by Kidane et al. [13] revealed that *O. europaea* tree is a multipurpose species in the study area. According to previous studies, the hard and heavy wood is useful for farm implements [25]. In addition, many households use *O. europaea* wood for firewood or making charcoal because it burns slowly and has a high calorific value with little smoke [10,26]. The chemical components of wood and leaves [27,28] make the tree attractive for fumigation and cleaning teeth. The logs used for farm implements were medium-sized, whereas there was no size preference for fuel wood. By contrast, large logs were preferred for fumigation, possibly because of the villagers' belief that large *O. europaea* logs had more effective medicinal value than did small ones. However, we could not find any evidence of suggested log size for fumigation use in previous studies.

The *O. europaea* stump diameter distribution shows that small trees were cut more frequently than were large ones, and the reason could be the population dynamics of the species, as similar size

distributions have been found in most non-regulated tree populations [29,30]. Therefore, the harvesting pattern might simply have been a result of natural availability. Another explanation could be that small trees were easier to cut with the tools available, and were therefore used for firewood [31]. During the interviews, we also noted that the local people did not have any special size preference regarding the species used for fuel wood. In addition, since the forest is at its secondary succession [12], perhaps any large trees in the reserve had been cut a long time ago.

The positive relationship between the harvesting rate and elevation may be due to the high abundance of the species at higher elevations. Kidane et al. [32] observed that the abundance of different tree species, including *O. europaea*, was higher at higher elevations in the same forest.

We found a positive relationship between the number of stumps and distance from the nearest village up to ca. 2.5 km, but for longer distances the relationship was weaker. This finding shows that most trees have been cut at intermediate distances (ca. 1.5–2.5 km) from the nearest village during recent years. According to Kidane et al. [13], sawmills were installed in the forest in the 1950s, and trees were harvested for commercial purposes. However, the decreasing number of stumps found beyond 3 km from the village probably related to transport economics, since *O. europaea* is heavy and transportation is very difficult, which often means that the wood has to be carried by hand.

Surprisingly, the market price for *O. europaea* wood in Mekelle was lower than in the villages around Hugumburda Forest, possibly due to high demand for the species by the local communities living around the forest [13]. It is probable that the *O. europaea* wood sold at the wood market in Mekelle comes from many sources, and competition among suppliers may help to keep the prices for the wood relatively low. In turn, this could increase the likelihood of illegal harvesting in forests.

Despite the existence of rules and regulations that prohibit the harvesting of *O. europaea* in Hugumburda Forest, local people continue using the wood regularly. This was particularly the case in Kukufto village, and the reason might be that most of the forest guards were from the village of Hashenge, which is near the forest. Thus, it was relatively easy for the guards to identify who among the people living in the closest villages had cut the trees, and the people were afraid of being caught. The people in the farthest village, Kukufto, might have had less fear about harvesting *O. europaea* wood in the forest because few forest guards were enrolled from their village. Furthermore, we observed that there were more *O. europaea* wood merchants in Kukufto than at Shoko Majo market because most of the forest guards were from Hashenge, and therefore they could be stricter towards those living in villages nearer to them than could other guards. This, in turn, may be a reason why we found a low probability of *O. europaea* wood being obtained directly from the forest by the villagers in Hashenge. It may be a good idea to recruit guards from all villages surrounding the reserve to make the forest guarding more secured. However, forest guards are employed to look after the forest reserve and ensure that illegal harvesting does not occur. Clearly, they have not been entirely effective in this respect, and this may be due to a lack of sufficient resources for patrolling or because guards are corrupt or unwilling to stop low-intensity tree cutting carried out by their own neighbors [33,34]. The level of patrolling necessary to stop all illegal harvesting may not be socially optimal [35]. Since the forest is at its secondary stage of development, which means it is dominated by small-sized woody species [13], we would not encourage any harvesting in the forest except for non-timber forest products. In addition, for an effective guarding system, we recommend that the forest administration should consider equal representation of guards from all surrounding villages.

5. Conclusions

Illegal harvesting of *O. europaea* wood was observed in Hugumburda Forest for three main uses, fuel wood, fumigation, and farm implements, likely because the local people did not have an alternative source. The positive relationship between the harvesting rate and elevation showed a high frequency of harvesting in the forest at higher altitudes, where *O. europaea* is abundant. The estimated value of *O. europaea* biomass harvested illegally does not seem to degrade the population of this tree

species. We recommend the establishment of permanent sample plots in the forest reserve in order to monitor the increment of *O. europaea* as well as other tree species.

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