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Seed production, seed dispersal and seedling establishment of two afromontane tree species in and around a church forest: implications for forest restoration

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Abstract

Background: Seed production, seed dispersal and seedling establishment are relevant life phases of plants. Understanding these processes and their patterns is essential to recognize vegetation dynamics and to apply it to forest restoration.

Methods: For *Olea europaea* and *Schefflera abyssinica*, fecundity was estimated using randomized branch sampling. Seed dispersal and seedling establishment were monitored using spatially explicit seed traps and plots. Dispersal functions were calibrated applying inverse modeling.

Results: *O. europaea* produced more seeds and had longer dispersal distances compared to *S. abyssinica*. Correlations between observed and predicted number of recruits were statistically significant. Seedlings of the two species showed different niche requirements.

Conclusions: The studied species were recruitment-limited due to low dispersal activity or lack of suitable microsites. Restoration relying on natural regeneration should overcome these limitations by increasing disperser visitation and reducing biotic and abiotic stresses.

Keywords: Fecundity, *Olea europaea*, *Schefflera abyssinica*, Recruitment limitation, Restoration

Background

Deforestation is almost a synonym for Ethiopian forest history. Small patches of forests that surround churches, hence called church forests, are the only remnants after past deforestation in the northern part of the highlands (Nyssen et al. 2004, 2009). Church forests are located as islands in a matrix of a highly degraded agricultural landscape (Wassie et al. 2005). They represent hotspots of biodiversity and are critical conservation areas in the Afromontane region (Aerts et al. 2016). Ecosystem restoration with the objective of watershed and riparian repair functions as well as livelihood and landscape diversification is a national priority in current land management in these degraded highlands (Nyssen et al. 2004).

The most appropriate strategy to restore degraded agricultural landscapes involves the reconstruction of native plant communities through re-colonization of native flora, reforestation or afforestation (Stanturf et al. 2014). Restoration can be achieved using tree species (active restoration), relying on natural re-colonization, or through assisted natural regeneration (passive restoration). Both approaches have been discussed as restoration options to re-vegetate the highlands of Ethiopia (Abiyu et al. 2011). In the past, reforestation programs with plantation species were successful due to the fast growth of such species and their well-known management practices (Zanne and Chapman 2001; Lemenih and Teketay 2006). While these plantations improve soil fertility (Lemma et al. 2006; Abiyu et al. 2011), they do not have any positive effect on biodiversity (Chazdon 2008) and therefore represent an incomplete first step of a restoration process (Stanturf et al. 2001). Assisted

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natural regeneration and natural regeneration rank highest on the restoration ladder (sensu Chazdon 2008) with the highest ranks in biodiversity and ecosystem services at the lowest associated cost. These approaches, however, have the highest requirements in terms of spatial distribution of residual vegetation or biological legacies (Bannister et al. 2014). In order to achieve cost-efficient and timely restoration, a combination of mixed passive and active restoration strategies are favored in certain situations (Bannister et al. 2014). Thus, strategies and methods of forest restoration may follow different paradigms depending on stakeholder objectives, regional climate and degree of degradation (Jacobs et al. 2015).

Fruit production, seed dispersal, germination and seedling establishment are critical life phases in plants (Harper 1997). A clear understanding of these issues are crucial to recognize patterns of colonization and extinction, directional changes in species composition or succession over time, which have strong relevance for ecosystem restoration (Hobbs et al. 2007). Information on relevant life phases of Afromontane plant species is scarce. In the absence of this information there are no means to identify the risks of failure of management measures and the means to overcome them. This information helps to understand filters of succession that determine the floristic composition of the secondary forest resulting from a passive restoration treatment. An understanding of these key processes allows the prediction of the likely outcome of any silvicultural measure in terms of vitality, density, survival, growth and quality of regeneration at an appropriate time (Wagner et al. 2010).

Studies on the regeneration ecology of trees in the Afromontane forest regions in Ethiopia have characterized propagule pools, particularly soil seed banks and seedling banks, thus focusing on storage effects of reproductive potentials (Teketay and Granström 1995, 1997). Soil seed banks have little potential as a source of tree regeneration in the Afromontane region given the lack of available seeds due to soil erosion or the failure to form persistent soil seed banks owing to the physiological requirements of seeds (Teketay and Granström 1995, 1997). Apart from a study carried out for *Leptonychia usambarensis* in Tanzania (Cordeiro et al. 2009), no studies have been conducted to characterize seed dispersal of tree species in Afromontane forests. Some studies conducted so far acknowledge the importance of this information for East African Afromontane forests (Aerts et al. 2006). In principle, recruitment limitation can be caused by limited seed availability or by constraints on seedling establishment (Clark et al. 1999, 2007; Nathan et al. 2000; Muller-Landau et al. 2002). Dispersal mediated recruitment limitation is especially severe with fleshy fruited trees (Rey and Alcántara 2000; Zywiec et al. 2013). While these limitations may promote coexistence in plant communities at stand levels (Herrera and Jordano 1981; Herrera et al. 1998; Abrams 2003), they severely inhibit ecosystem restoration (Holl 1998, 1999, 2008).

Ecosystem restoration in general requires knowledge on seed dispersal characteristics of targeted tree species and an understanding of constraints to seedling establishment and survival. The objective of this study was to compare the similarities and differences between the seed dispersal, seed rain and seedling establishment patterns of two selected native tree species in an Afromontane church-forest of the northern Ethiopian Highlands.

Methods
Study area
The research was conducted in and around Tara-Gedam church forest in northwestern Ethiopia (12°08′35′′N and 37°44′29′′E), situated in steep mountain terrain. The northern and northwestern boundaries of the forest are defined by steep hill slopes, the western boundary by a highway. The southern and the southeastern boundaries delimit it towards a matrix of farm and grazing land settled by subsistence farmers. Leaving a diversity of trees, which have positive interaction with crops and livestock scattered in the landscape (parkland agroforestry), is a typical land use system. The elevation ranges from 2175 to 2390 m. The mean annual minimum temperature is 13 °C and the maximum 27 °C. The mean annual rainfall is 1085 mm and occurs from June to September. The composition of the forest consists of the following native trees and shrubs: *Olea europaea* L. ssp. *cuspidata* (Wall. ex G. Don) Cif., *Schefflera abyssinica* (Hochst. ex A. Rich.) Harms, *Albizia schimperiana* Oliv., *Ekebergia capensis* Sparrm., *Croton macrostachyus* Hochst. ex Del., *Acacia negrii* Pic.-Serm., *Apodytes dimidiata* E. Mey. ex Arn., *Nuxia congesta* R. Br. ex Fresen., *Schrebera alata* (Hochst.) Welw., *Grewia ferruginea* Hochst. ex A. Rich., *Vernonia amygdalina* Del., *Calpurnia aurea* (Ait.) Benth., *Carrisa spinarum* L., *Dovyalis abyssinica* (A. Rich.) Warb., *Bersama abyssinica* Fresen., *Rhus glutinosa* A. Rich., *Clausena anisata* (Willd.) Benth., *Osyris quadripartita* Decn., *Maesa lanceolata* Forssk. and *Myrsine africana* L. *Eucalyptus camaldulensis* Dehn. is the dominant non-native tree species in the matrix of degraded land beyond the church forest.

Two native tree species, i.e., *Olea europaea* L. ssp. *cuspidata* (Wall. ex G. Don) Cif. (from here on referred to as *O. europaea*) and *Schefflera abyssinica* (Hochst. ex A. Rich.) Harms (*S. abyssinica*) were selected for this study, considering their dominance as upper canopy trees in forest remnants and also for their timber and non-timber importance to local people. The study was carried out from February to November 2009 and from January to October 2010.

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O. europaea is an evergreen tree or shrub, reaching a height of up to 18 m. The flowers and fruits are clustered on auxiliary panicles. Fruits are dark violet when ripe, one seeded and 0.5 to 1 cm in diameter. Flowering and fruiting time is between September and January. Dispersal is predominantly by frugivorous birds. *S. abyssinica* is a deciduous tree species reaching up to a height of 30 m. The flowers and fruits are clustered at the end of 30 to 40 cm racemes. The multi-seeded fruits are red and 0.26 to 0.31 cm long. Flowering and fruiting time is from March to May. Dispersal is mostly carried out by fruit eating birds (Bamps 1989). In our study area, it starts its life as an epiphyte and becomes an upper canopy tree when fully grown (Abiyu et al. 2013).

### Seed trap placement for dispersal distance estimation

Seed traps were used to sample seed rain inside and outside the forest patch. The seed traps were circular baskets with a 60 cm radius, made from bamboo and lined with plastic sheets. Three 1.5-m high stakes were used to raise the seed traps above the ground to avoid predation by rodents (Additional file 1). However, not all traps were at similar height above the ground, given differences caused by pit preparation.

Traps were arranged inside the forest and in the matrix outside the forest. In the matrix outside the forest, traps were arranged along transects, under trees and along water bodies and drainage lines (Fig. 1). The total number of traps set inside and outside the forest was 388. The coordinates (x, y) of each trap and potential seed source tree were established. The traps were set up in November 2009 and were monitored during the fruit setting period up to July 2010. Seeds from traps were collected once a week, counted at the spot, bagged, labeled and transported to the laboratory. This routine was repeated until no more seeds were recovered from the traps.

Regeneration study

Next to each trap, 1 m^2 (1 m × 1 m) plots were prepared, where seeds were marked with toothpicks and monitored for emerging seedlings. These plots were stratified into: (i) open habitats, (ii) stones/boulders, (iii) trees/shrubs and (iv) banks and the immediate neighborhood of water bodies (springs, ponds and creeks).

While established plants and germinants are rare in the studied habitats, tree establishment was observed in
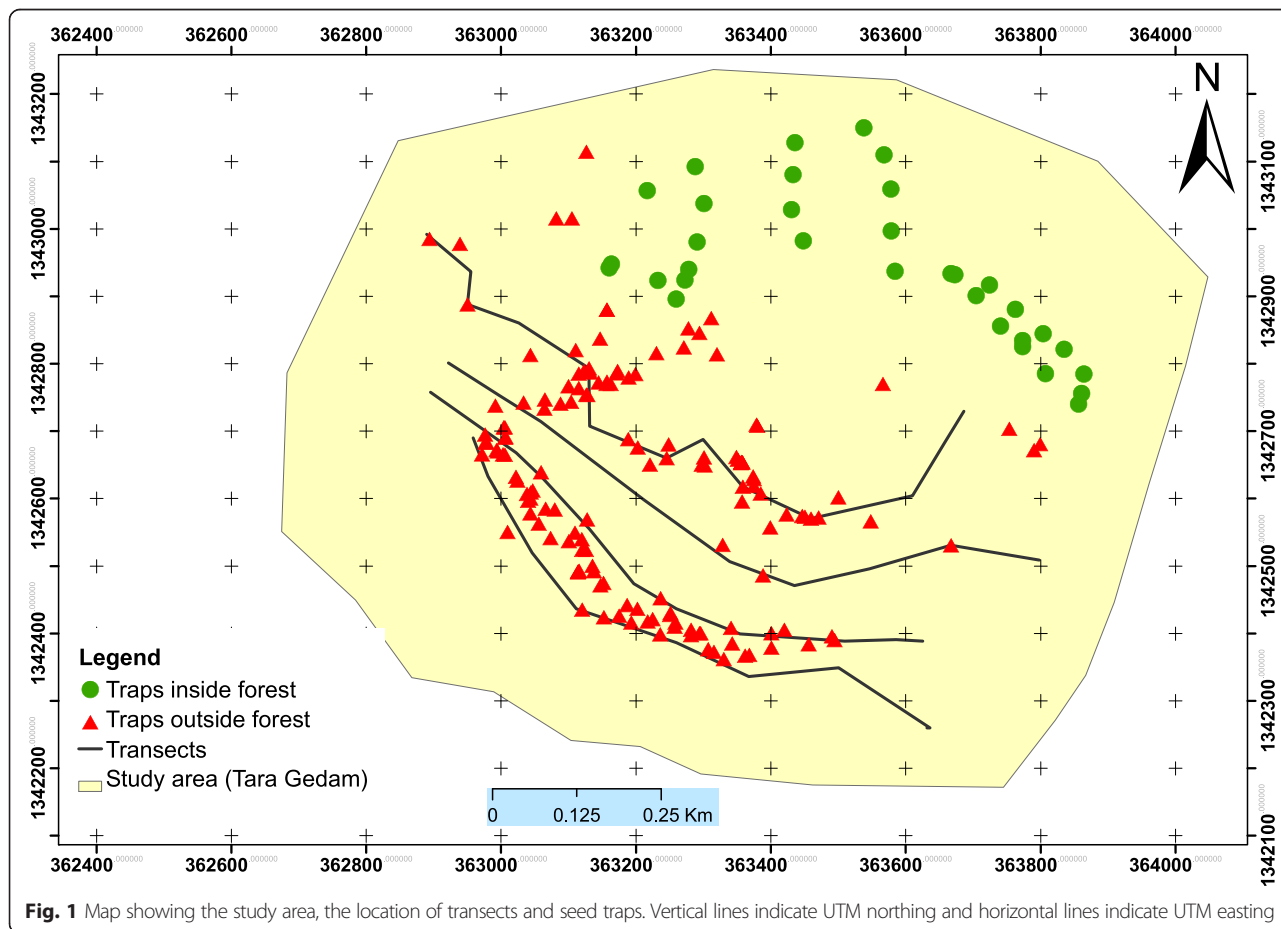
Fig. 1 Map showing the study area, the location of transects and seed traps. Vertical lines indicate UTM northing and horizontal lines indicate UTM easting

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areas with freshly exposed soil by human activity. In addition and in order to validate seed dispersal kernels with plant distribution, we laid out a further set of 34 square plots (2 m × 2 m) along additional transects running from seed sources into the open habitats, perpendicular to the first set of transects. Habitats for these plots were classified into road side boulders (12 plots), stone bunds on farms (10 plots) and open spaces between these habitats (12 plots).

Modeling seed dispersal: fecundity and distance

The approach developed by Ribbens et al. (1994) is widely used in modeling seed dispersal (Loiselle et al. 1996; Wada and Ribbens 1997; LePage et al. 2000; Canham and Uriarte 2006). It models both components of dispersal functions, i.e., the amount of seeds produced and the dispersal distance. Poisson distribution functions are used to predict the seedling recruitment patterns using the following equation:

$$R = \left[STR \times \left(\frac{dbh}{45} \right)^{\beta} \right] \times \frac{1}{n} \times \left[e^{-D \times m^{\theta}} \right] \qquad (1)$$

where R is the predicted number of recruits (seeds and seedlings) and STR (standard total recruitment) denotes the number of fruits produced by a tree of standard dbh (diameter at breast height). The parameter β modifies STR as a power function of the actual dbh observed.

The second part of the equation represents the mean density of recruits in a trap located at distance m from the parent tree, where n is a normalizer ensuring that the area under the second portion of the equation is equal to 1,   determines the shape of the distribution and D determines the steepness of decline in the number of recruits as the distance from the parent tree increases. Therefore, the number of recruits (R) predicted for trap i, given T trees, is:

$$R_i = \sum_{j=1}^{T} \left[STR \times \left(\frac{dbh_j}{45} \right)^{\beta} \right] \times \frac{1}{n} \times \left[e^{-D \times m_{ij}^{\theta}} \right] \qquad (2)$$

where m_{ij} is the distance from the i_{th} sample trap to the j_{th} tree.

Fecundity estimation

We used randomized branch sampling (RBS) for the initial estimation of fecundity or standard total recruitment (STR) (Gregoire et al. 1995). RBS is a multistage sampling procedure, which defines a unidirectional random walk along the natural branching pattern within the crown of a tree. In this procedure, the most important points are defining the nodes (points where branching begins), segments (inter-nodal points) and paths (series of successive segments). A path is selected starting from the first node. The following segment is chosen by randomized selection weighted by the relative cross sectional area (CSA) of the radiating segments on the node. The thicker the segment, the more likely its selection. Eight individual trees of both species were randomly selected, since the church limited destructive sampling. From each individual tree, a limb (segment) was chosen from a pair or couple of limbs (segments) according to the probability proportional to its CSA. The number of seeds on the chosen limb (segment) was counted. This process continued until a terminal limb (segment), with a predetermined specific size was reached. The terminal limb circumference was between 4 and 6 cm. Fecundity then is defined as the total number of fruit counts at the final stage of the selected limb divided by the product of probabilities along the path (Jessen 1955; Cancino and Saborowski 2005, 2007; Peter et al. 2010). The total number of seeds per tree varied from 7,000 to 110,000 for both species.

Thus, the initial value of STR was set at 50,000 and the fixed dbh was set at 45 cm based on the average value of sampled trees. Initial values for the parameters were made to fluctuate and wander up to 40 % of their original values, without fixing them, as suggested by E. Ribbens (personal communications).

Data analysis

Model evaluation

Models were evaluated using maximum likelihood estimation, resulting in a likelihood function, which states the probability of obtaining a set of observations. In our case, maximum likelihood based dispersal functions determined the probability to observe a certain number of seeds, given a particular set of parameters. RECRUITS 3.1 (Ribbens 2002) was used to calibrate the dispersal function (equation 2), using the Metropolis algorithm to find a combination of parameter values that are likely to produce the observed values.

Mean dispersal distance (MDD), percentage of strange recruits or percentage strangers (PS), observed-predicted correlation and confidence intervals were calculated for the statistical evaluation of the model. RECRUITS calculates MDD by distributing the expected seeds on a circle around a parent tree and determining the average distance from the tree. The observed-predicted correlation is the measure of spatial association between observed and model predicted values; this method uses product—moment correlation coefficients between observed values and expected means for every species. Approximate bivariate 95 % confidence intervals were fitted for estimates of STR and MDD values using the inverse likelihood ratio test. The percentage strangers (PS) calculates the amount of seeds contributed by trees outside the observation distance or the amount of seeds

contributed from unmapped trees in the vicinity of the traps inside the observation distance.

Model validation

The recruitment functions (equation 2) were cross-validated by omitting every third trap, computing a new model and using the new model to predict traps omitted from the new model (Ribbens et al. 1994).

Regeneration study

Descriptive statistics were used to visualize the number of seeds reaching different traps located in the various habitats. In the 2 m × 2 m plots along the transects, one way ANOVA with unequal sample sizes was used to test the hypothesis of differences between the various habitats (micro sites) in the emergence of seedlings.

Results and Discussion

The amounts of seeds produced per parent tree varied between the two species. The STR value denoting the seed production for the standardized parental size was higher for *O. europaea* (36,219) than for *S. abyssinica* (28,221) (Table 1).

The standard total recruitment (STR) values show seed production potential and hence fecundity. The total seed production values for both species studied are within the range of estimates of fruit production reported for tropical trees in Africa, e.g., 12,000–72,000 reported from Cameroon (Norghauer and Newbery 2015). Clark et al. (2005) estimated the fecundity of trees in the Dja Reserve, Cameroon between 25,000 to 65,000 for bird dispersed seeds and from 22,000 to 79,000 for mammal dispersed seeds.

Seed dispersal profiles of the two species showed that up to 55 m dispersal distance seed densities were higher for *S. abyssinica* than for *O. europaea*, while the latter species had higher seed densities compared to *S. abyssinica* at longer distances (Fig. 2).

The difference in the dispersal profile of the two tree species may be a reflection of the reproductive ability of their mother trees, their seed disperser activity and differential requirements of the seeds and seedlings (Rey and Alcántara 2000). *S. abyssinica* is represented by few large and sparsely scattered trees in the forest (Abiyu et al. 2013). It produces lipid and protein rich fruits (Saracco et al. 2005) with attractive colors which can be tracked by specialist and generalist frugivorous birds, probably with short gut retention time, dropping the seeds close to the seed source. *O. europaea* trees are distributed abundantly in the study area. Their fruits are mostly tracked by specialized frugivorous birds, which may disperse the seeds over longer distances.

The median distance was 200 m for *O. europaea* and 100 m for *S. abyssinica*. The mean dispersal distance (MDD) was 191 m for *O. europaea* and 92 m for *S. abyssinica* (Table 1). The percentage of strangers was higher for *O. europaea* (46 %) than for *S. abyssinica* (40 %).

Dispersal distances for both species can be included in the range of long distance dispersal (Norghauer and Newbery 2015), even though they are shorter than reported by other studies from the tropics. Clark et al. (2005) found up to 473 m dispersal distances for animal-dispersed species. Farther distances (316 m) were also reported (Godoy and Jordano 2001). In general, animal dispersed tree species seeds have longer dispersal distances than wind dispersed ones (Ribbens et al. 1994).

The number of predicted and observed recruits are shown for both species (Fig. 3). The correlation coefficient, indicating intensity of association or spatial congruence between observed and predicted data sets, was

Table 1 Maximum likelihood estimates of the parameters used in the dispersal function

Parameter	*Olea europaea* (median dispersal distance 200 m)			*Schefflera abyssinica* (median dipersal distance 100 m)		
	Mean	Confidence interval		Mean	Confidence interval	
		Lower	Upper		Lower	Upper
STR[a]	36, 219	35, 600	38, 500	28, 221	26, 900	28, 900
Beta	1.08	0.96	1.19	0.94	0.84	1.03
D[b]	2.43	2.39	2.46	12.06	11.74	12.37
MDD[c]	191	188.7	198.5	92	88.9	95.2
Theta	0.46	0.46	0.46	0.78	0.77	0.78
R[d]	0.38*			0.39*		
Normalizer	5684			7328		

Beta and Theta are parameters for the Poisson distribution function
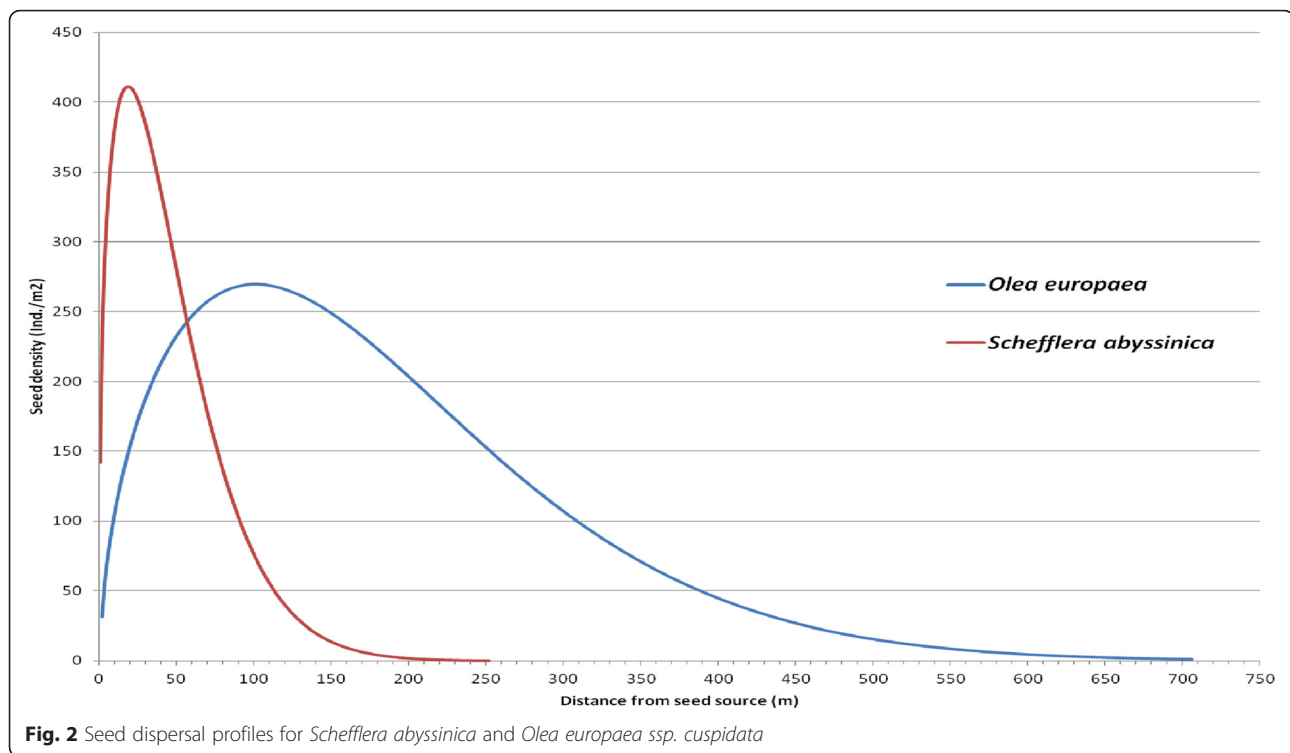*Significant at $p = 0.05$
[a]STR is the standard total recruitment
[b]D the speed of the decline in the number of recruits
[c]MDD the mean dispersal distance
[d]R the observed-predicted correlation

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Fig. 2 Seed dispersal profiles for *Schefflera abyssinica* and *Olea europaea ssp. cuspidata*

0.38 for *O. europaea* and 0.39 for *S. abyssinica* (Table 1). These values were also statistically significant when cross-validated, i.e., 0.55 for *O. europaea* and 0.35 for *S. abyssinica*. The highest number of dispersed seeds was located near their source trees (Fig. 4).

Despite the arrival of seeds, there was no seedling recruitment on the 1 m^2 plots located near to the seed traps. Seeds of *S. abyssinica* were found in traps placed under fruiting trees of its own species, while no seeds were found in traps placed in other habitats. The highest average number of seeds of *O. europaea* per trap was recorded in traps placed close to springs (681) followed by traps adjacent to bigger stones (183), under trees/shrubs (22) and on open sites (<1) (Table 2).

No seedling recruitment from the ground was recorded for *S. abyssinica* in the 2 m × 2 m plots. There were no statistically significant ($F = 2.29$, $p = 0.12$) differences in the number of seedlings of *O. europaea* among the various habitats. However, a large number of *O. europaea* seedlings were found on human-made structures such as between boulders excavated during road construction and on stone bunds constructed for soil and water conservation (Fig. 4). On these selected habitats, seedling density diminished with increasing distance from the seed source.

Except on certain human-made structures, seed dispersal was not accompanied by successful germination. Two conditions, non-random arrival and survival in

predictable locations, should be met for directed seed dispersal to occur. Therefore, its contribution is minimal for vegetation dynamics in the study area. This may arise mainly from the uncoupling of different selective forces acting on seeds and seedlings (Rey and Alcántara 2000) or from onthogenic shifts in stress and resource requirement in various microhabitats (Jordano and Herrera 1995; Schupp 1995).

O. europaea and *S. abyssinica* are recruitment-limited in our studied landscape. Although there are several mother trees at the population level for the production of recruits for *O. europaea*, this species is recruitment-limited due to low dispersal activity as well as its failure to germinate and establish after dispersal. Dispersers birds do not take seeds of *O. europaea* to microsites. On the other hand, *S. abyssinica* is recruitment-limited because there are few mother trees at the population level and too few available microsites such as branch forks and stem wounds. These available microsites can be saturated easily (Abiyu et al. 2013).

The location of restoration sites in relation to the seed source critically affects restoration success (Holl 1998, 1999, 2008). Our study corroborates the need to maintain patches of forests as islands and stepping stones for biodiversity conservation and restoration. Church forests in northern Ethiopia are remnants of the original tree population (Aerts et al. 2016). Currently, these forests are facing strong anthropogenic pressure and dispersal

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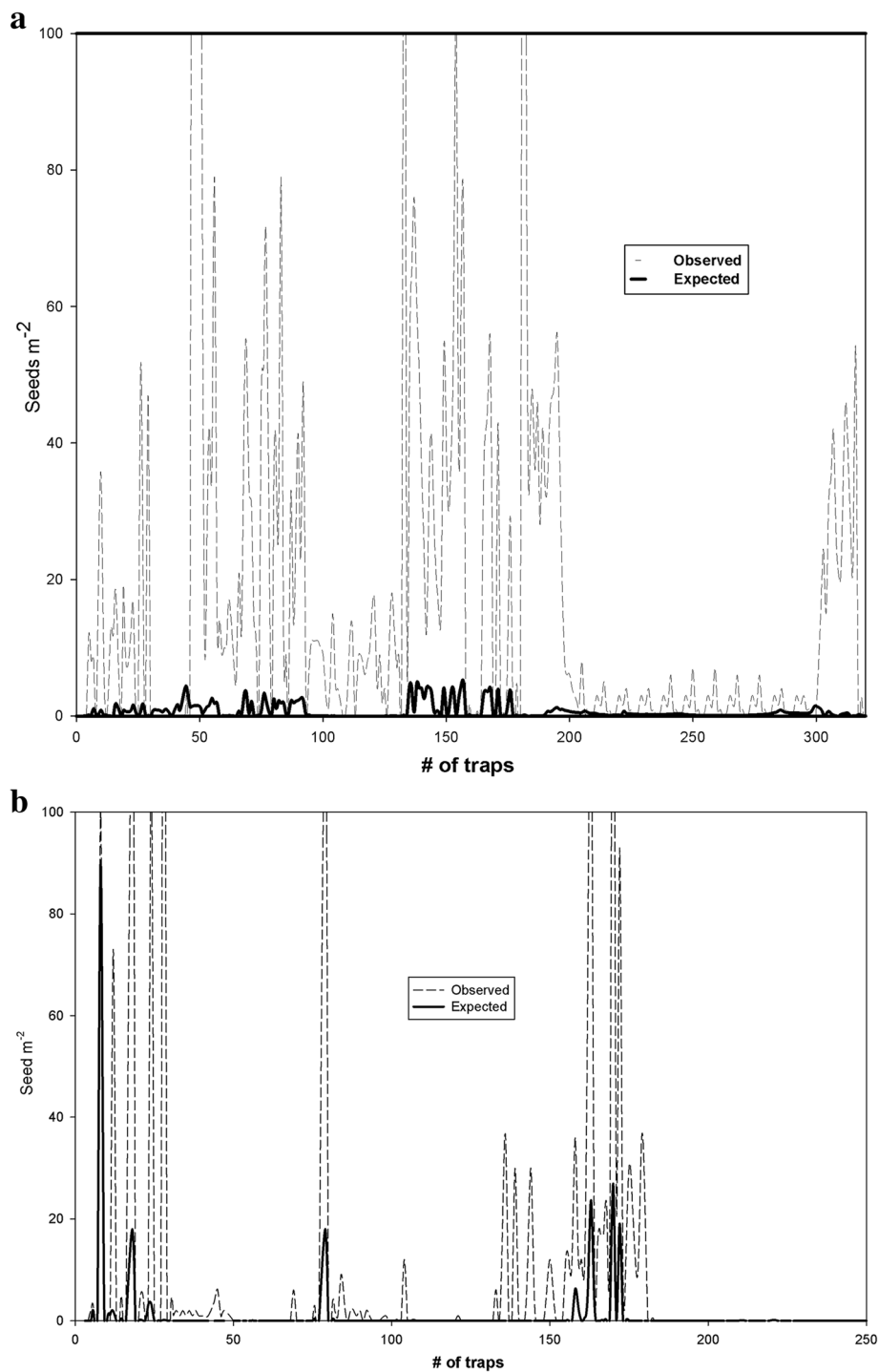
Fig. 3 Predicted (continuous lines) and observed (dotted lines) seed density of **a** *Olea europaea* ssp. *cuspidata* and **b** *Schefflera abyssinica*

of propagules from these remnants is crucial to form viable populations at the patch level. As well, restoration of those areas, devoid of their natural vegetation in the landscape, need seed input from the remnant forests. Seed dispersal is a filter for succession and affects the

quality of regeneration in the context of passive restoration. This raises the importance of other landscape elements and biological legacies, such as trees on hedges and homesteads to support restoration as seed sources. In the absence of these supplementary seed sources,

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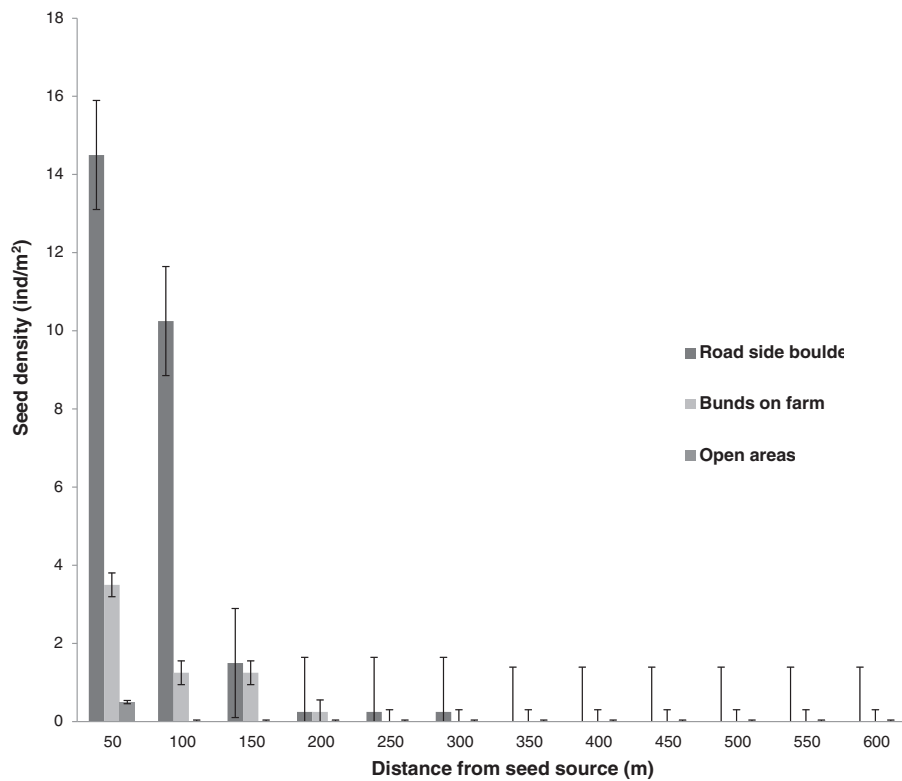
Fig. 4 Seed density of *Olea europaea* seedlings on artificially created structures as a function of distance from the seed source

deliberate introduction of these two species may be needed in highly degraded areas.

Conclusions

The median dispersal distance for both species is less than 200 m. For successful dispersal and recruitment of *O. europaea* and *S. abyssinica* in degraded ecosystems in the Ethiopian highlands, the potential mother trees should be located not farther than the median dispersal distance. In the absence of seed sources within the indicated distance, reliance on natural regeneration may not be a suitable restoration strategy.

Table 2 Mean number of seeds recorded in seed traps placed in different habitats for *Olea europaea* ssp. *cuspidata* and *Schefflera abyssinica* (the numbers in brackets indicate the standard deviation of the mean)

Habitat for trap location	Number of traps with seeds	Mean number of seeds per trap	
		Olea europaea	*Schefflera abyssinica*
Open	158	0.18 (0.89)	-
Stone/boulders	32	183 (755)	-
Trees/shrubs	230	22 (53)	43 (48)
Springs	11	681 (1580)	-

Additional file

Additional file 1: Seed traps. (PPTX 3274 kb)

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References

Abiyu A, Gratzer G, Teketay D, Glatzel G, Aerts R (2013) Epiphytic recruitment of *Schefflera abyssinica* (A. Rich) Harms. and the rle of microsites in affecting tree community structure in remnant forests in northwest Ethiopia. SINET: Ethiopian J Sci 36(1):41–44

Abiyu A, Lemenih M, Gratzer G, Aerts R, Teketay D, Glatzel G (2011) Status of native woody species diversity and soil characteristics in an exclosure and in plantations of *Eucalyptus globulus* and *Cupressus lusitanica* in Northern Ethiopia. Mt Res Dev 31(2):144–152

Abrams MD (2003) Where has all the white oak gone? Bioscience 53(10):927–939

Aerts R, van Overtveld K, November E, Wassie A, Abiyu A, Demissew S, Daye DD, Giday K, Haile M, TewoldeBerhan S, Teketay D, Teklehaimanot Z, Binggeli P, Deckers J, Friis I, Gratzer G, Hermy M, Heyn M, Honnay O, Paris M, Frank JS, Muys B, Bongers F, Healey JR (2016) Conservation of the Ethiopian church forests: Threats, opportunities and implications for their management. Sci Total Enviro 551:404–414

Aerts R, Maes W, November E, Negussie A, Hermy M, Muys B (2006) Restoring dry Afromontane forest using bird and nurse plant effects: Direct sowing of *Olea europaea* ssp. *cuspidata* seeds. Forest Ecol Manage 230(1–3):23–31

Bamps R (1989) Araliaceae. In: Hedberg I, Edwards S (eds) Flora of Ethiopia, vol 3, Addis Abeba University. Addis Abeba & Uppsala University, Uppsala, Addis Abeba, pp 537–543

Bannister JR, Wagner S, Donoso PJ, Bauhus J (2014) The importance of seed trees in the dioecious conifer *Pilgerodendron uviferum* for passive restoration of fire disturbed southern bog forests. Aust Ecol 39(2):204–213

Cancino J, Saborowski J (2005) Comparison of randomized branch sampling with and without replacement at the first stage. Silva Fennica 39(2):201–216

Cancino J, Saborowski J (2007) Improving RBS estimates–effects of the auxiliary variable, stratification of the crown, and deletion of segments on the precision of estimates. J For Sci 53(7):320–333

Canham CD, Uriarte M (2006) Analysis of neighborhood dynamics of forest ecosystems using likelihood methods and modeling. Ecol Appl 16(1):62–73

Chazdon RL (2008) Beyond deforestation: restoring forests and ecosystem services on degraded lands. Science 320(5882):1458–1460

Clark C, Poulsen J, Bolker B, Connor E, Parker V (2005) Comparative seed shadows of bird-, monkey-, and wind-dispersed trees. Ecology 86(10):2684–2694

Clark C, Poulsen J, Levey D, Osenberg C (2007) Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. Am Nat 170(1):128–142

Clark J, Beckage B, Camill P, Cleveland B, HilleRisLambers J, Lichter J, McLachlan J, Mohan J, Wyckoff P (1999) Interpreting recruitment limitation in forests. Am J Bot 86(1):1–16

Cordeiro NJ, Ndangalasi HJ, McEntee JP, Howe HF (2009) Disperser limitation and recruitment of an endemic African tree in a fragmented landscape. Ecology 90(4):1030–1041

Godoy JA, Jordano P (2001) Seed dispersal by animals: exact identification of source trees with endocarp DNA microsatellites. Mol Ecol 10(9):2275–2283

Gregoire TG, Valentine HT, Furnival GM (1995) Sampling methods to estimate foliage and other characteristics of individual trees. Ecology 76(4):1181–1194

Harper JL (1997) Population biology of plants. Academic, London

Herrera CM, Jordano P (1981) *Prunus mahaleb* and birds: the high-efficiency seed dispersal system of a temperate fruiting tree. Ecol Monogr 51(2):203–218

Herrera CM, Jordano P, Guitián J, Traveset A (1998) Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationship to pollination and seed dispersal. Am Nat 152(4):576–594

Hobbs RJ, Jentsch A, Temperton VM (2007) Restoration as a process of assembly and succession mediated by disturbance. In: Walker LR, Walker J, Hobbs RJ (eds) Linking restoration and ecological succession. Springer, New York, pp 150–167

Holl KD (1998) Do bird perching structures elevate seed rain and seedling establishment in abandoned tropical pasture? Restor Ecol 6(3):253–261

Holl KD (1999) Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. Biotropica 31(2):229–242

Holl KD (2008) Are there benefits of bat roosts for tropical forest restoration? Conserv Biol 22(5):1090

Jacobs DF, Oliet JA, Aronson J, Bolte A, Bullock JM, Donoso PJ, Landhäusser SM, Madsen P, Peng S, Rey-Benayas JM (2015) Restoring forests: What constitutes success in the twenty-first century? New Forests 46(5–6):601–614

Jessen RJ (1955) Determining the fruit count on a tree by randomized branch sampling. Biometrics 11(1):99–109

Jordano P, Herrera CM (1995) Shuffling the offspring: uncoupling and spatial discordance of multiple stages in vertebrate seed dispersal. Écoscience 2:230–237

Lemenih M, Teketay D (2006) Changes in soil seed bank composition and density following deforestation and subsequent cultivation of a tropical dry Afromontane forest in Ethiopia. Trop Ecol 47(1):1–12

Lemma B, Kleja DB, Nilsson I, Olsson M (2006) Soil carbon sequestration under different exotic tree species in the southwestern highlands of Ethiopia. Geoderma 136(3–4):886–898

LePage PT, Canham CD, Coates KD, Bartemucci P (2000) Seed abundance versus substrate limitation of seedling recruitment in northern temperate forests of British Columbia. Can J For Res 30(3):415–427

Loiselle BA, Ribbens E, Vargas O (1996) Spatial and temporal variation of seed rain in a tropical lowland wet forest. Biotropica 28(1):82–95

Muller-Landau HC, Wright SJ, Calderón O, Hubbell SP, Foster RB (2002) Assessing recruitment limitation: concepts, methods and case-studies from a tropical forest. In: Levey DJ, Silva WR, Galetti M (eds) Seed dispersal and frugivory: ecology, evolution and conservation. CABI Publishing, Wallingford, pp 35–53

Nathan R, Safriel UN, Noy-Meir I, Schiller G (2000) Spatiotemporal variation in seed dispersal and recruitment near and far from *Pinus halepensis* trees. Ecology 81(8):2156–2169

Norghauer JM, Newbery DM (2015) Tree size and fecundity influence ballistic seed dispersal of two dominant mast-fruiting species in a tropical rain forest. For Ecol Manage 338:100–113

Nyssen J, Haile M, Naudts J, Munro N, Poesen J, Moeyersons J, Frankl A, Deckers J, Pankhurst R (2009) Desertification? Northern Ethiopia re-photographed after 140 years. Sci Total Environ 407(8):2749–2755

Nyssen J, Poesen J, Moeyersons J, Deckers J, Haile M, Lang A (2004) Human impact on the environment in the Ethiopian and Eritrean highlands—a state of the art. Earth Sci Rev 64(3–4):273–320

Peter H, Otto E, Hubert S (2010) Leaf area of beech (*Fagus sylvatica* L.) from different stands in eastern Austria studied by randomized branch sampling. Eur J For Res 129(3):401–408. doi:10.1007/s10342-009-0345-8

Rey PJ, Alcántara JM (2000) Recruitment dynamics of a fleshy fruited plant (*Olea europaea*): connecting patterns of seed dispersal to seedling establishment. J Ecol 88(4):622–633

Ribbens E (2002) RECRUITS 3.1 Operating manual. Department of Biology. Western Illinois University, Macomb

Ribbens E, Silander JA, Pacala SW (1994) Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. Ecology 75(6):1794–1806. doi:10.2307/1939638

Saracco JF, Collazo JA, Groom MJ, Carlo TA (2005) Crop size and fruit neighborhood effects on bird visitation to fruiting *Schefflera morototoni* trees in Puerto Rico. Biotropica 37(1):81–87

Schupp EW (1995) Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. Am J Bot 82:399–409

Stanturf JA, Palik BJ, Dumroese RK (2014) Contemporary forest restoration: A review emphasizing function. For Ecol Manage 331:292–323

Stanturf JA, Schoenholtz SH, Schweitzer CJ, Shepard JP (2001) Achieving restoration success: myths in bottomland hardwood forests. Restor Ecol 9(2):189–200

Teketay D, Granström A (1995) Soil seed banks in dry Afromontane forests of Ethiopia. J Veg Sci 6(6):777–786

Teketay D, Granström A (1997) Germination ecology of forest species from the highlands of Ethiopia. J Trop Ecol 13(6):805–831

Wada N, Ribbens E (1997) Japanese maple (*Acer palmatum* var. *matsumurae*, Aceraceae) recruitment patterns: seeds, seedlings, and saplings in relation to conspecific adult neighbors. Am J Bot 84(9):1294–1300

Wagner S, Collet C, Madsen P, Nakashizuka T, Nyland RD, Sagheb-Talebi K (2010) Beech regeneration research: from ecological to silvicultural aspects. For Ecol Manage 259(11):2172–2182

Wassie A, Teketay D, Powell N (2005) Church forests provide clues to restoring ecosystems in the degraded highlands of Northern Ethiopia. J Ecol Rest 23(2):131–132

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Zanne AE, Chapman CA (2001) Expediting reforestation in tropical grasslands: distance and isolation from seed sources in plantations. Ecol Appl 11:1610–1621

Zywiec M, Holeksa J, Wesolowska M, Szewczyk J, Zwijacz-Kozica T, Kapusta P (2013) *Sorbus aucuparia* regeneration in a coarse-grained spruce forest–a landscape scale. J Veg Sci 24(4):735–743