Biodivers Conserv (2017) 26:209–221
DOI 10.1007/s10531-016-1239-y

ORIGINAL PAPER

Stone walls and sacred forest conservation in Ethiopia

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Received: 11 January 2016 / Revised: 6 October 2016 / Accepted: 21 October 2016 /

Abstract Many tropical forests worldwide are protected due to their sacredness to religious communities. In the south Gondar region of Ethiopia, most of the remaining native forests are tiny fragments (5.42 ha ± 0.34) surrounded by pasture and agriculture that are protected because they encompass churches of the Ethiopian Orthodox Tewahido Church (EOTC). A small number of communities have erected stone walls around the perimeter of the forests to demarcate the boundary, and/or protect the interior of the forest. We evaluated the effectiveness of these walls at protecting ecological conditions by examining tree and seedling communities among sacred forests with and without walls in Montane and Upper Montane sites. We found the wall to be an effective conservation tool as regeneration potential was higher in forests with a wall. The density and species richness of seedlings were significantly higher in forests with a wall and these effects were more pronounced in Upper Montane forests. Forests with a wall also had seedlings of many native tree species that were not found in forests without walls. As expected, there were few differences in tree communities in forests with and without a wall. Although rare on

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Communicated by Frank Chambers.

This article belongs to the Topical Collection: Forest and plantation biodiversity.

Electronic supplementary material The online version of this article (doi:10.1007/s10531-016-1239-y) contains supplementary material, which is available to authorized users.

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the landscape, the presence of a stone wall around these forests was effective at protecting the seedling community because it likely reduced access to the forests by grazers and directed human visitors to trails. The use of a stone wall may protect seedling communities in other sacred forest fragments, particularly for those that are small, isolated, surrounded by agriculture, and have a depleted seed bank.

Keywords Afromontane forest · Church forest · Deforestation · Forest fragmentation · Regeneration potential · Seedlings

Introduction

All over the world, species, sites or entire forests are protected because of their sacredness to religious communities (Dudley et al. 2009). These protected areas can outnumber legally conserved areas in some tropical countries and in some cases are more effective at protecting natural resources than legally conserved areas (UNESCO 2003; Chatterjee et al. 2004; Dudley et al. 2009). These sacred conservation sites are important for conserving cultural diversity (Bhagwat and Rutte 2006) and offer opportunities for the conservation of tropical biodiversity in areas threatened by deforestation and fragmentation (Cardelús et al. 2012). The conservation value of sacred sites and forests has often been assessed by indices of biodiversity, such as the number of total or endemic species (Mwikomeke et al. 2000; Mgumia and Oba 2003; Bossart et al. 2006). While measuring species richness and the number of endemic species in sacred forests is valuable, such metrics only provide a snapshot of the forest in its current state and do not directly address how changes might be occurring through time. To examine the potential for long-term persistence of these sacred forests on the landscape we need to examine their potential for forest regeneration.

Changes in socioeconomic status and land use in developing regions can lead to increased degradation and deforestation (Mascia et al. 2014). As a result, sacred forests in developing regions are often small, fragmented and situated in agricultural landscapes (Gadgil and Vartak 1975; Bhagwat and Rutte 2006). In a study examining the impact of land-use change on sacred forests (known as church forests in Ethiopia) in the Gamo Highlands of southern Ethiopia, there was a 36.6% decrease in forest area and 109.4% increase in agricultural lands and human settlements between 1995 and 2010 (Daye and Healey 2015). The sacred forests in the Gamo Highlands exhibited less reduction in forest area (5.7 %) than non-sacred forest (43.2 %) over the same period indicating the effectiveness of religious management of forests (Daye and Healey 2015). However, with less forest cover overall, the continued persistence of these forests on the landscape could be threatened from increasing fragmentation.

Forest fragments are often more degraded than intact forest because of the high degree of edges that create an artificial and hard boundary and cause ecological changes (Laurance et al. 2011). Microclimates are altered more at the edges than in the interior of the forest including having higher wind, higher temperature, and lower relative humidity (Laurance et al. 1998b), which result in elevated rates of mortality for trees and seedlings (Laurance et al. 1998a; Bruna 2002; Zambrano et al. 2014), particularly of specialist or disturbance-sensitive native species (Laurance et al. 1998a; Lobo et al. 2011). The high perimeter-to-area ratios of forest fragments also enable greater access to forests by people seeking resources and grazing cattle from adjoining agricultural fields, which can negatively impact the seedling community (Wassie et al. 2009b). Furthermore, forest fragments that are isolated often lack seed sources (Jorge and Garcia 1997; Benitez-Malvido 1998), which can compromise the long-term persistence of forests, particularly for small fragments. Thus, regeneration potential, the recruitment of seedlings, of sacred forests may be threatened due to the high degree of fragmentation, the small size of the forests, the isolation from seed sources, human disturbance, and edge effects (Jorge and Garcia 1997; Teketay 1997; Benitez-Malvido 1998; Cardelús et al. 2013).

In the South Gondar region of northern Ethiopia, the majority of the native forest exists as tiny fragments that surround churches and monasteries of the Ethiopian Orthodox Tewahido Church (EOTC). Sacred forests are an integral component of the church as they provide sites for religious ceremonies, social gatherings, and burial grounds (Klepeis et al. in press). The sacred forests are small with an average area of 5.42 ha (±0.34 SE) and are isolated as they are surrounded by a matrix of agriculture and pasture, and are separated from one another by approximately 2 km (Bongers et al. 2006; Cardelús et al. 2013). Although individual sacred forests in northern Ethiopia average only 9.8 woody plant species (Aerts et al. 2006), these forests cumulatively have the highest tree diversity in the region, 91 (Wassie and Teketay 2006), and are refugia for many of northern Ethiopia's endangered endemic plant and invertebrate taxa (Aerts et al. 2006; Bongers et al. 2006). These forests are, therefore, regional biodiversity hotspots (Bongers et al. 2006). Like other sacred forests, Ethiopian sacred forests have exhibited remarkable resilience in the face of disturbance as only 0.4 % of 1022 forests measured in the South Gondar region have disappeared over the last half-century (Cardelús et al. in review).

Despite the persistence of sacred forests on the landscape, the high degree of isolation and external pressures, such as those from grazing animals and humans, may be negatively affecting forest regeneration potential. In a study assessing the seed banks of seven sacred forests in northern Ethiopia, seeds of only five (6 %) of the 91 woody species recorded in the forests were found in the soil bank indicating that regeneration of these forests from seeds would be threatened by the removal or loss of large, native tree species, a consequence of forest fragmentation as discussed above (Laurance et al. 2000; Wassie and Teketay 2006). However, while seedling establishment of four species of native trees including *Juniperus procera* (Cupressaceae), *Ekebergia capensis* (Meliaceae), *Prunus africana* (Rosaceae), and *Olea europaea* ssp. *cuspidata* (Olinieaceae) in these forests was found to be extremely low in open fields after seed sowing, seedling establishment was relatively high in local canopy openings in the forest and along forest edges, indicating some native trees have the potential to regenerate if their seedling communities are protected (Wassie et al. 2009a). Grazing herds of cows, sheep, and goats gain access to the forest through unprotected forest edges and browse, step on and graze the seedling community (Teketay 1997; Wassie et al. 2009b). Wassie et al. (2009a) demonstrated that livestock exclusion increased seedling survivorship and seedling growth for four native tree species (Wassie et al. 2009b). They also found that people living close to the forests entered the forest interior in search of fuel wood, which can damage and disturb the seedling community.

In response to disputes over land tenure and ownership, as well as forest extent, a small number of churches have erected a stone wall around their forests for multiple reasons: low walls are used to designate the church land boundary and are fairly common whereas larger walls capable of preventing cattle from grazing on or near burial grounds are rare. These larger walls are valued not only because of the protection they provide but because they add prestige to the churches (Klepeis et al. in press). We evaluated the effectiveness of these larger walls in preserving the regeneration potential of sacred forests by examining the tree and seedling communities in sacred forests in Ethiopia with and without a wall.

Given that the walls are a recent addition to the landscape (approximately 1–10 years) and native tropical trees can live up to hundreds of years, we predicted that there would be large differences in the seedling community (species richness, abundance, and composition) but little to no differences in the tree community in forests with and without a wall. We also examined the extent of human disturbance, which we defined as the presence of buildings, paths or trails, graves, or gathering areas where trees have been removed, in forests with and without a wall to determine if the presence of a wall reduces human disturbance.

Methods

Study area

Our study was conducted in the South Gondar Administration Zone of the Amhara National Regional State in Northern Ethiopia (14,607 km^2, 11°N 41′34″, 37°E 48′11″). The forest type is afromontane with a mean annual rainfall of 1216 mm and an average daily temperature of 19 °C (Wassie et al. 2009a). The wet season is from June to August and the dry season is from September to May, however March, April and May can also have some precipitation (Wassie et al. 2009a).

We established three 10 × 10 m long-term plots in 13 sacred forests in South Gondar. In previous research we found that forests closer to markets (i.e., <50 km from a city) had a higher degree of disturbance than forests far from markets (Cardelús et al. in review). To evaluate the effectiveness of stone walls on the richness and abundance of the tree and seedling communities as well as on the reduction of human disturbance, we confined our study to forests close to market. From a survey of over 100 sacred forests, we chose forests that represented the regional average in size and had a similar surrounding matrix (e.g., no forest bordered a lake). We gained permission to conduct research in the forests from both the church leaders and local authorities. Our study forests had an average area of 7.1 ha (±1.10 SE), which is larger than the regional average of 5.2 ha (±0.44 SE) (Cardelús et al. 2013). The forests close to markets were found along two elevation bands and were classified as either Montane (1700–2100 m asl) or Upper Montane (2400–2800 m asl). We had seven montane forests sites, three of which had a wall and four without, and six upper montane forest sites, three of which had a wall and three that did not. Montane forests are dominated by *Millettia ferruginea* (Fabaceae), *Mimusops kummel* (Sapotaceae), and *Teclea nobilis* (Rutaceae) and Upper Montane forests are dominated by *Carissa edulis* (Apocynaceae), *Euphorbia abyssinica* (Euphorbiaceae) and *J. procera* (Cupressaceae) (Wassie et al. 2009a).

Survey

To measure the tree communities within each forest, we identified, tagged and measured every tree >10 cm diameter at breast height (dbh) within each of the three forest plots. To measure the density (number of individuals) and species richness (number of species) of seedlings, within each plot we established three 1 m × 1 m seedling plots that fell along the diameter line of the plot from the NE corner to the SW corner, in which we identified and counted seedlings of woody species <10 cm height. We chose seedlings <10 cm height to ensure that the seedlings we counted were less than the age of the wall, which varied among our sites, but all of which are at least 2 years old. We estimated that any seedling <10 cm would be <2 years old based on previous research on the yearly growth rate of four tree species including *J. procera* (Cupressaceae), *E. capensis* (Meliaceae), *P. africana* (Rosaceae), and *O. europaea* ssp. *cuspidata* (Olinieaceae) to be 0.6–1.2 cm/year (Wassie et al. 2009a).

To measure the percent of human disturbance, we conducted three modified Gentry transects at three cardinal directions 0°, 120° and 240° from the church center towards the edge of the forest (Gentry 1988). Each transect was 2 m wide and the length varied with forest size (45–438 m). Along each transect we identified all native woody species >1 cm dbh and recorded human disturbances, which included trails, buildings, grave sites, or other human effects (e.g., wood piles). We calculated the percent of each transect that was designated as human disturbance (% disturbance) (Cardelús et al. in review). We also calculated the % human disturbance in each forest for the minimum transect length we measured (45 m) in order to standardize the size of the transect in each forest.

Statistical analysis

We used analysis of variance (ANOVA) to examine the influence of the presence of a wall and elevation on seedling density, seedling species richness, tree density, tree species richness, and % human disturbance (2-way ANOVA). To meet the assumptions of ANOVA, density and richness values were log(x + 1) transformed and % human disturbance was arcsine square-root transformed prior to analysis. We used 2-sample *t* tests to examine the effects of a wall within each elevation on seedling and tree density, seedling and tree species richness, and % human disturbance. We also calculated the non-parametric richness estimator Chao2 that is based on the presence/absence of species to estimate species richness for both trees and seedlings by plot with 100 randomizations using the EstimateS program (Chazdon et al. 1998; Colwell 2013). We used ANOVA to examine differences in Chao2 seedling and tree richness among forests with and without a wall at each elevation. Elevation was treated as a categorical explanatory variable with two classes: Montane and Upper Montane.

We used non-metric multidimensional scaling (NMDS) to examine differences in species composition of trees and seedlings between all forests within each elevational zone with a wall and without a wall. We used Monte-Carlo permutation tests to examine the stress of the NMDS. For each NMDS, we only included forests for which there was more than one individual and we only included species that were found in at least 2 forests resulting in 11 forests and 38 species included in the analysis. We used R v. 3.0.2 for all of our statistical analyses and the metaMDS function in the vegan package for our NMDS (R Development Core Team 2009; Oksanen et al. 2010).

Results

A total of 64 woody plant species from 57 genera and 36 families were recorded within all 13 forests. In total, 586 individual seedlings from 37 different species and 296 individual trees from 54 different species were measured (Online Resource 1). Average (±SE) seedling density in forests without a wall was 1.7 ± 0.7 and in forests with a wall was 9.0 ± 2.4. Average tree density in forests without a wall was 5.3 ± 1.2 and in forests with a wall was 10.2 ± 1.6. We counted a total of 383 seedlings from 27 seedling species and

113 individual trees from 31 tree species in Montane forests (Online Resource 1). Upper Montane forests had 203 seedlings from 20 species and 183 trees from 32 tree species.

Seedlings

Overall, seedling density in our study forests was significantly higher in all forests with a wall than without a wall (2-way ANOVA: $F_{1,12} = 16.8$, $P = 0.003$) regardless of elevation, which had no significant effect (2-way ANOVA: $F_{1,12} = 1.0$, $P = 0.4$; Fig. 1a). However, this effect was driven by Upper Montane forests in which seedling density was significantly higher in forests with a wall than without a wall (*t* test: $t = -5.3$, df = 4, $P = 0.006$) as seedling density was not significantly influenced by a wall in Montane forests (*t* test: $t = -2.3$, df = 5, $P = 0.07$; Fig. 1a).

Seedling species richness was significantly higher in all sites with a wall than without a wall (2-way ANOVA: $F_{1,12} = 31.8$, $P < 0.001$), and the effect of the wall on seedling species richness did not vary with elevation (2-way ANOVA: $F_{1,12} = 2.1$, $P = 0.2$; Fig. 1b). Seedling species richness was significantly higher in forests with a wall than without a wall in both Montane (*t* test: $t = -3.5$, df = 5, $P = 0.02$) and Upper Montane forests (*t* test: $t = -5.4$, df = 5, $P = 0.006$; Fig. 1b). Chao2 seedling richness followed a similar trend as it was significantly higher in all sites with a wall than without a wall (2-way ANOVA: $F_{1,12} = 20.2$, $P = 0.0015$), and did not vary with elevation (2-way ANOVA: $F_{1,12} = 0.1$, $P = 0.7$).

Additionally, forests with walls had different seedling species composition. In the Montane region, forests with a wall had more tree species that had seedlings in the same

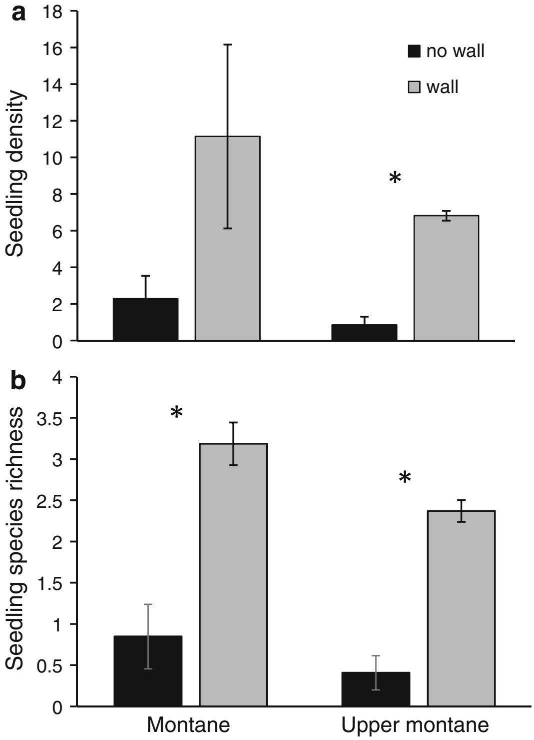

Fig. 1 Average (±SE) seedling density (**a**) and seedling species richness (**b**) in three 1 m^2 subplots in each of three 10 m^2 plots (9 subplots in total) in sacred forests with a large stone wall built around the forest or not in Montane forest (1700 to 2175 m asl) and Upper Montane forest (2410 to 2800 m asl) in the South Gondar region of Ethiopia. There were seven forests in the Montane region, three of which had a wall and six forests in the Upper montane region, three of which had a wall. The *asterisk* symbol denotes significant differences with and without a wall within an elevation according to 2-sample *t* tests ($P < 0.05$). There was no significant elevation effect

site (32 %) than forests without a wall (16 %). The tree species that were regenerating in sites with a wall but were not found in sites without a wall included *Rhus vulgaris* (Anacardiaceae), *Combretum molle* (Combretaceae), and *Canthium oligocarpum* (Rubiaceae) (Online Resource 1). For some species in Montane forests, the wall had no effect as they were found in forests with and without a wall including *Albizia schimperiana* (Fabaceae), *M. ferruginea*, *M. kummel*, and *T. nobilis* (Online Resource 1).

In the Upper Montane forests, the number of trees that had seedlings in the same site was higher in forests with a wall (35 %) than in forests without a wall (12 %). Species that were regenerating only in sites with a wall included Agave (*Asparagaceae*), *O. europaea* ssp. *cuspidata* (Olinieaceae), *P. africana* (Rosaceae) and *T. nobilis* (Online Resource 1). Species that were found as seedlings in sites with and without a wall included *Clausena anisata* (Rutaceae) and *Dovyalis abyssinica* (Flacourticaceae) (Online Resource 1).

Seedling species composition differed among sites with and without a wall at both elevations, which was driven by the differences in tree species that were regenerating only in forests with a wall (Fig. 3).

Trees

Tree density was significantly impacted by the presence of a wall (2-way ANOVA: $F_{1,12} = 13.9$, $P = 0.005$, Fig. 2a) but this did not vary with elevation (2-way ANOVA: $F_{1,12} = 0.1$, $P = 0.8$). The influence of a wall on tree density was driven by the Montane

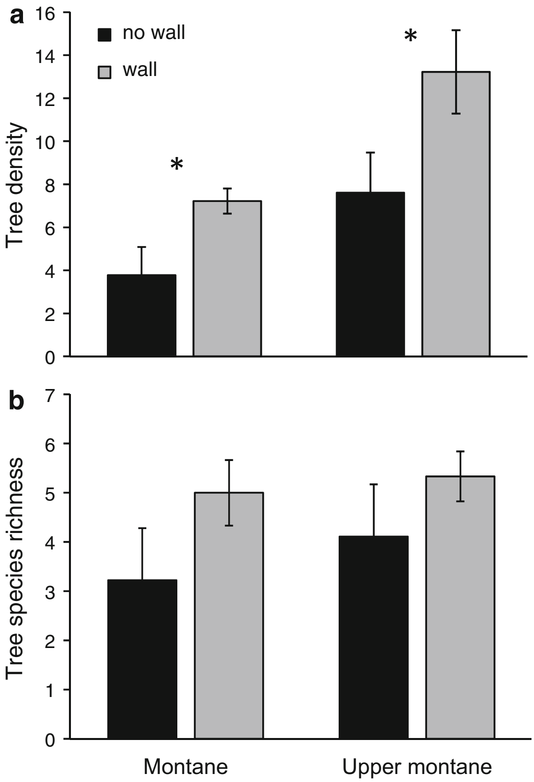

Fig. 2 Average (±SE) tree density (**a**) and tree species richness (**b**) in three 10 m^2 plots in sacred forests with a large stone wall built around the forest or not in Montane forest (1700 to 2175 m asl) and Upper Montane forest (2410 to 2800 m asl) in the South Gondar region of Ethiopia. There were seven forests in the Montane region, three of which had a wall and six forests in the Upper montane region, three of which had a wall. The *asterisk* symbol denotes significant differences with and without a wall within an elevation according to 2-sample *t* tests ($P < 0.05$). Tree density was significantly higher in the Upper Montane sites than in the Montane sites ($P = 0.007$)

forests where tree density was significantly higher with a wall (t test: $t = -2.7$, df = 5, $P = 0.04$). Tree density was not different between forests with and without a wall in Upper Montane forests (t test: $t = -2.1$, df = 4, $P = 0.1$). Tree density was significantly impacted by elevation as it was significantly higher in the Upper Montane forests than in the Montane forests (2-way ANOVA: $F_{1,12} = 12.4$, $P = 0.007$, Fig. 2a).

Tree species richness was not significantly influenced by the presence of a wall (2-way ANOVA: $F_{1,12} = 5.0$, $P = 0.05$), elevation (2-way ANOVA: $F_{1,12} = 0.9$, $P = 0.4$) nor the interaction between wall and elevation (2-way ANOVA: $F_{1,12} = 0.3$, $P = 0.6$, Fig. 2b). Chao2 tree richness was also not significantly influenced by the presence of a wall (2-way ANOVA: $F_{1,12} = 3.5$, $P = 0.1$), elevation (2-way ANOVA: $F_{1,12} = 0.2$, $P = 0.6$) or their interaction (2-way ANOVA: $F_{1,12} = 0.2$, $P = 0.7$).

As predicted, tree species composition did not differ among sites with and without a wall in any elevation (Fig. 3). Thus, any differences in seedling species composition were likely driven by the presence of a wall. However, several tree species were found in forests for which no seedlings were found in any of our 13 forests regardless of whether or not a wall was present including *Celtis africana* (Ulmnaceae), *Croton macrostachyus* (Euphorbiaceae), and *J. procera* in the Montane region and *J. procera* and *Stephania abyssinica* (Menispermaceae) in the Upper Montane region (Online Resource 1).

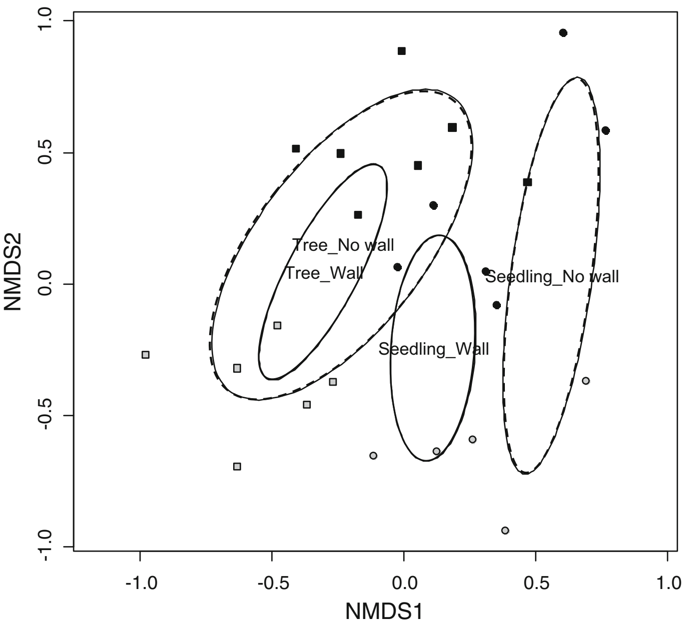

Fig. 3 Non-metric multidimensional scaling ordination of seedling (*circles*) and tree (*squares*) species composition for the seven Montane sites (*black symbols*; range of 1700 to 2175 m asl), and for the six Upper Montane sites (*grey symbols*; range of 2410 to 2800 m asl) with a large stone wall built around the forest (*solid lines*) or not (*dashed lines*) in the South Gondar region of Ethiopia. Ellipses show the standard deviation of point scores around each category (trees and seedlings with and without wall). Three forests at each elevation had a wall. One Montane site and one Upper Montane site had no seedlings and were, therefore, removed from the analysis

Disturbance

The presence of a wall significantly influenced the mean percent human disturbance and this depended on elevation (2-way ANOVA: $F_{1,12} = 23.6$, $P < 0.001$). In the Montane sites, human disturbance was significantly higher in the forests with a wall than without a wall (t test: $t = -4.0$, df = 5, $P = 0.01$) while the opposite was found in the Upper Montane sites where disturbance was significantly lower with a wall (t test: $t = 3.0$, df = 4, $P = 0.04$, Fig. 4). When considering the same length of transect in each forest (45 m), the relationship between forests with and without a wall in each elevation did not differ from our analyses using the entire transect, which indicates that the differences we detected in human disturbances were due to the presence of a wall and not the differences in area sampled; however total human disturbance increased on average by 26 % when considering only the first 45 m of each transect indicating a greater human presence in the forest closest to the church.

Discussion

We found that small sacred forest fragments in northern Ethiopia with a large stone wall had higher regeneration potential than forests without a wall. Sacred forests with a wall surrounding them had significantly higher seedling species richness than forests without a wall at both elevations and seedling density was significantly higher with a wall in the Upper Montane forests. These data indicate that the presence of a wall reduces disturbances to the seedling community through reducing edge effects, reducing grazing by livestock (Online Resource 2, Wassie et al. 2009b) and/or reducing human access to the

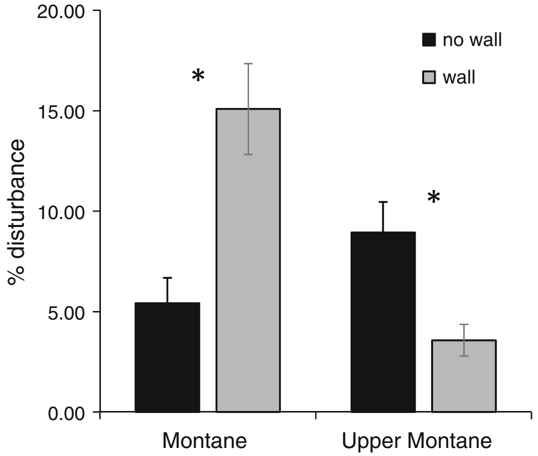

Fig. 4 Mean (±SE) percent human disturbance in sacred forests with a large stone wall built around the forest or not in Montane forest (1700 to 2175 m asl) and Upper Montane forest (2410 to 2800 m asl) in the South Gondar region of Ethiopia. There were seven forests in the Montane region, three of which had a wall and six forests in the Upper montane region, three of which had a wall. The *asterisk* symbol denotes significant differences with and without a wall within an elevation according to 2-sample t tests ($P < 0.05$). Percent human disturbance was significantly higher in the Montane sites than in the Upper Montane sites ($P = 0.03$)

forest interior, and that these effects vary with elevation. The effect of the wall on seedling communities in the Upper Montane forests, for example, was possibly driven by the reduced human disturbance in forests with a wall. In the Montane forests, counter-intuitively, there was significantly higher human disturbance in forests that had a wall, which indicates a larger human presence in those forests (Fig. 4). Despite a larger human presence, seedling species richness and tree density in Montane forests were higher with a wall than without. Given that we chose our plots in forested areas away from trails, the higher seedling richness and tree density in the Montane forests with a larger human presence indicates that these forests are regenerating and the wall is directing human visitors to trails rather than the forest interior. Because human disturbance was found to be higher closer to the church, directing human visitors away from the forest interior is particularly important for the smallest forests (<4 ha). Erecting a wall around the forest could maintain the regeneration potential of sacred forests, which is vital for the long-term persistence of these forests and the preservation of the endangered and endemic taxa (Bongers et al. 2006) along with the preservation of essential ecosystem services to the surrounding community, such as fresh water, shade and pollinators (Cardelús et al. 2012).

The floristic composition of the seedling community differed in sites with and without a wall at both elevations, and the presence of a wall enabled the regeneration of some species that are known to have low regeneration status. For example, *O. europaea* ssp. *cuspidata* is known to have poor regeneration in the South Gondar Zone (Wassie et al. 2009a; Zegeye et al. 2011). Seedlings of *O. europaea* ssp. *cuspidata* were not found in forests without a wall, confirming its low regeneration status, but they were found in forests with a wall indicating the importance of the wall for the continued presence of this species in these forests. Other species were not influenced by the wall and showed regeneration in all forests including *P. africana*, which was also found to have low regeneration status (Wassie et al. 2009a), *M. ferruginea*, which is endemic to Ethiopia, *M. kummel* and *T. nobilis*. Other species were not regenerating in any of the forests with or without a wall including *J. procera*, a shade-tolerant, endemic, old-growth species that has low regeneration status even with livestock exclusion (Wassie et al. 2009b), and *R. albersii* that has poor regeneration in the Lake Tana region (Alelign et al. 2007). Thus, forests with a wall were less degraded than forests without a wall as they had a more abundant and diverse seedling community, particularly for species with low regeneration status. However, these forests may require more active restoration efforts, such as planting, for species that were not regenerating in forests with a wall.

Releasing tropical forests from grazing pressures can help promote the recovery of native vegetation. In sacred forests of the South Gondar region of Ethiopia, seed germination, seedling survival and seedling growth were higher in forests that excluded livestock by building fenced enclosures than forests that allowed access to livestock (Wassie et al. 2009b). In Hawaiian tropical dry forest, forests with grazers excluded for 40 years had greater native plant diversity and regeneration than forests without grazer exclusion (Cabin et al. 2000). This could explain the greater density and species richness of seedlings in sacred forests with a wall that excluded grazers than without a wall. Furthermore, livestock and grazers could be changing forest composition by selectively grazing particular species, which may explain the differences in seedling species composition between sites with and without a wall. Foraging selectivity by grazers often drives changes in the dominance of particular species because species with high leaf nutrient concentrations and low chemical defenses are preferentially selected (Allen et al. 1984; Augustine and McNaughton 1998; Mason et al. 2010). Seedlings of native tree species *R. vulgaris*, *C. mollie*, and *C. oligocarpum*, for example, were abundant in sites with a wall and rare in sites without a wall whereas seedlings of other native tree species, including *T. nobilis*, *M. ferruginea*, *M. kummel*, and *D. abyssinica* were found in forests with and without a wall. If grazers are selectively grazing on particular seedlings, such as *R. vulgaris* or *C. mollie*, their continued presence in forests without a wall may be compromised. Grazers can also have strong impacts on vegetation structure at the tree stage (Spear and Chown 2009), which could influence the future of these forests because stand regeneration depends on an abundant and viable seed supply (Kozlowski 2002). Given the limited seed bank of native tree species in sacred forests (Wassie and Teketay 2006) and the difficulty of seed dispersion between isolated fragments (Jorge and Garcia 1997), the continued presence of large seed-producing native trees and their seedlings in these forests is imperative for the continued persistence of these forests on the landscape.

We found that the regenerative capacity of sacred forest fragments was higher in forests with a wall than without a wall, and the use of large stone walls in Ethiopia as well as in other tropical regions may enhance the ability of sacred forest fragments to regenerate. However, walls were not traditionally used to protect sacred forests and most churches in the South Gondar region do not have walls at all. Some churches have low and incomplete walls that are older and were used to demarcate the church boundary (Klepeis et al. in press), which could be improved to protect the regeneration of these forests. Those communities that have built the new walls examined in our study did so for different reasons, including status, a desire to protect grave sites from livestock, and to delineate definitively land controlled by the church (Klepeis et al. in press). Thus, we recognize that any effort to use walls as a conservation strategy should be part of community-based initiatives. We also acknowledge that building a wall around a forest fragment may impede forest expansion. Thus, the use of a barrier to protect forest regeneration should be considered as a short-term strategy in places where forests are at high risk of degradation, such as those whose seedling communities are at risk from grazing and trampling, and for those that are small, isolated, and have a depleted seed bank. Walls would be particularly useful for small forest fragments surrounded by a matrix of agriculture with low quality residual vegetation (Chazdon 2003, 2008), given the importance of the landscape matrix in the recovery of degraded forests (Chazdon 2003).

In order to examine the effectiveness of sacred sites for biodiversity conservation for the long term, we need to move beyond measures of species richness and the number of endemic species. While other management practices may be effective at preserving the sacred forests and their endemic species that currently exist on the landscape, such as establishing national policies for sacred forest management (Juhé-Beaulaton 2008) or incorporating sacred forests into already established protected forest networks (Bhagwat and Rutte 2006), few strategies mention conserving the seedling communities. The protection of the seedling community in sacred sites needs to be considered in evaluating their effectiveness at conserving biodiversity. Preserving the seedling community will ensure the capacity of the forests to regenerate and maintain biodiversity as well as sustain the livelihoods of the surrounding communities in isolated remnant tropical forest patches in light of ever increasing anthropogenic pressures on tropical forests worldwide.

Acknowledgements We would like to thank Ethiopian Orthodox Tewahido Church Diocese officials, respected church priests and monks in South Gondar for allowing us to conduct research in their sacred forests. We would also like to thank undergraduate students K. Jensen and J. Hair for help with field work. This research was supported by a grant to the authors from the Picker Interdisciplinary Science Institute at Colgate University.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Aerts R, Van Overtveld K, Haile M et al (2006) Species composition and diversity of small Afromontane forest fragments in northern Ethiopia. Plant Ecol 187:127–142

Alelign A, Teketay D, Yemshaw Y, Edwards S (2007) Diversity and status of regeneration of woody plants on the peninsula of Zegie, northwestern Ethiopia. Trop Ecol 48:37–49

Allen RB, Payton IJ, Knowlton JE (1984) Effects of ungulates on structure and species composition of the Urewera forests as shown by exclosures. N Z J Ecol 7:119–130

Augustine DJ, McNaughton SJ (1998) Ungulate effects on functional species composition of plant communities: Herbivore selectivity and plant tolerance. J Wildl Manag 62:1165–1183

Benitez-Malvido J (1998) Impact of forest fragmentation on seedling abundance in a tropical rain forest. Conserv Biol 12:380–389

Bhagwat SA, Rutte C (2006) Sacred groves: potential for biodiversity management. Front Ecol Environ 4:519–524

Bongers F, Wassie A, Sterck FJ et al (2006) Ecological restoration and church forests in northern Ethiopia. J Drylands 1:35–44

Bossart JL, Opuni-Frimpong E, Kuudaar S, Nkrumah E (2006) Richness, abundance, and complementarity of fruit-feeding butterfly species in relict sacred forests and forest reserves of Ghana. Biodivers Conserv 15:333–359

Bruna EM (2002) Effects of forest fragmentation on *Heliconia acuminata* seedling recruitment in central Amazonia. Oecologia 132:235–243

Cabin RJ, Weller SG, Lorence DH et al (2000) Effects of long-term ungulate exclusion and recent alien species control on the preservation and restoration of a Hawaiian tropical dry forest. Conserv Biol 14:439–453

Cardelús CL, Lowman MD, Wassie Eshete A (2012) Uniting Church and Science for Conservation. Science 335:916–917

Cardelús CL, Scull P, Hair J et al (2013) A preliminary assessment of Ethiopian sacred groves at the landscape and ecosystem scales. Diversity 5:320–334

Cardelús CL, Scull P, Wassie Eshete A, Woods CL, Klepeis P, Kent E, Orlowska I (in review) Shadow conservation and the persistence of church forests in northern Ethiopia. Biotropica

Chatterjee S, Gokhale Y, Malhotra KC, Srivastava S (2004) Sacred groves in India: an overview. Indira Gandhi Rashtriya Manav Sangrahalaya, Bhopal

Chazdon RL (2003) Tropical forest recovery: legacies of human impact and natural disturbances. Perspect Plant Ecol Evol Syst 6:51–71

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

Chazdon RL, Colwell RK, Denslow JS, Guariguata MR (1998) Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of NE Costa Rica. In: Dallmeier F, Comiskey JA (eds) Forest biodiversity research, monitoring and modelling: conceptual background and Old World case studies. Parthenon Publishing Group, Paris, pp 285–309

Colwell RK (2013) EstimateS: Statistical estimation of species richness and shared species from samples. Version 9 and earlier. User's Guide and application

Daye DD, Healey JR (2015) Impacs of land-use change on sacred forests at the landscape scale. Glob Ecol Conserv 3:349–358

Dudley N, Higgins-Zogib L, Mansourian S (2009) The links between protected areas, faiths, and sacred natural sites. Conserv Biol 23:568–577

Gadgil M, Vartak V (1975) Sacred groves of India: a plea for continued conservation. J Bombay Nat Hist Soc 72:313–320

Gentry AH (1988) Changes in plant community diversity and floristic composition on environmental and geographical gradients. Ann Missouri Bot Gard 75:1–34

Jorge LAB, Garcia GJ (1997) A study of habitat fragmentation in southeastern Brazil using remote sensing and geographic information systems (GIS). For Ecol Manag 98:35–74

Juhé-Beaulaton D (2008) Sacred forests and the global challenge of biodiversity conservation: the case of Benin and Togo. J Study Relig Nature, Cult 2:351–372

Klepeis P, Orlowska IA, Kent EF, et al Ethiopian Church Forests: A Hybrid Model of Protection. Hum Ecol (in press)

Kozlowski TT (2002) Physiological ecology of natural regeneration of harvested and disturbed forest stands: implications for forest management. For Ecol Manag 158:195–221

Laurance WF, Ferreira LV, Rankin-de Merona JM et al (1998a) Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. Conserv Biol 12:460–464

Laurance WF, Ferreira LV, Rankin-de Merona JM, Laurance SG (1998b) Rain forest fragmentation and the dynamics of Amazonian tree communities. Ecology 79:2032–2040

Laurance WF, Delamonica P, Laurance SG et al (2000) Rainforest fragmentation kills big trees. Nature 404:836

Laurance WF, Camargo JLC, Luizão RCC et al (2011) The fate of Amazonian forest fragments: a 32-year investigation. Conserv Biol 144:56–67

Lobo D, Leão T, Melo FP et al (2011) Forest fragmentation drives Atlantic forest of northeastern Brazil to biotic homogenization. Divers Distrib 17:287–296

Mascia MB, Pailler S, Krithivasan R et al (2014) Protected area downgrading, downsizing, and degazettement (PADDD) in Africa, Asia, and Latin America and the Caribbean, 1900–2010. Biol Conserv 169:355–361

Mason NWH, Peltzer DA, Richardson SJ et al (2010) Stand development moderates effects of ungulate exclusion on foliar traits in the forests of New Zealand. J Ecol 98:1422–1433

Mgumia FH, Oba G (2003) Potential role of sacred groves in biodiversity conservation in Tanzania. Environ Conserv 30:259–265

Mwikomeke ST, Msangi TH, Mabula CK, Nummelin M (2000) Plant species richness in the traditionally protected forests of Zigua, Handeni district, Tanzania. Silva Carelica 34:178–193

Oksanen J, Guillaume Blanchet F, Kindt R, et al (2010) Vegan: community ecology package

R Development Core Team (2009) R: a language and environment for statistical computing

Spear D, Chown SL (2009) Non-indigenous ungulates as a threat to biodiversity. J Zool 279:1–17

Teketay D (1997) Seedling populations and regeneration of woody species in dry Afromontane forests of Ethiopia. For Ecol Manag 98:149–165

UNESCO (2003) Linking universal and local values: managing a sustainable future for World Heritage. Paris

Wassie A, Teketay D (2006) Soil seed banks in church forests of northern Ethiopia: implications for the conservation of woody plants. Flora Morphol Distrib Funct Ecol Plants 201:32–43

Wassie A, Sterck FJ, Teketay D, Bongers F (2009a) Tree regeneration in church forests of Ethiopia: effects of microsites and management. Biotropica 41:110–119

Wassie A, Sterck FJ, Teketay D, Bongers F (2009b) Effects of livestock exclusion on tree regeneration in church forests of Ethiopia. For Ecol Manag 257:765–772

Zambrano J, Coates R, Howe HF (2014) Effects of forest fragmentation on the recruitment success of the tropical tree *Poulsenia armata* at Los Tuxtlas, Veracruz, Mexico. J Trop Ecol 30:209–218

Zegeye H, Teketay D, Kelbessa E (2011) Diversity and regeneration status of woody species in Tara Gedam and Abebaye forests, northwestern Ethiopia. J For Res 22:315–328