Conservation of the Ethiopian church forests: threats, opportunities and implications for their management

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Church forests in the Ethiopian highlands

small, isolated patches
patch size ≈2.5 ha
≈2 km between patches
≈25 woody species/patch

148 woody spp.
78 forests

NMDS

ELEVATION

NE   SW
PRECIPITATION, DIVERSITY
HUMAN POPULATION

complex shape
less diverse
more degraded
secondary species

round shape
more diverse
less degraded
indigenous conifers

Title Page

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Conservation of the Ethiopian church forests: threats, opportunities and implications for their management

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Abstract

In the central and northern highlands of Ethiopia, native forest and forest biodiversity is almost confined to sacred groves associated with churches. Local communities rely on these 'church forests' for essential ecosystem services including shade and fresh water but little is known about their region-wide distribution and conservation value. We (1) performed the first large-scale spatially-explicit assessment of church forests, combining remote-sensing and field data, to assess the number of forests, their size, shape, isolation and woody plant species composition, (2) determined their plant communities and related these to environmental variables and potential natural vegetation, (3) identified the main challenges to biodiversity conservation in view of plant population dynamics and anthropogenic disturbances, and (4) present guidelines for management and policy. The 394 forests identified in satellite images were on average ~2 ha in size and generally separated by ~2 km from the nearest neighboring forest. Shape complexity, not size, decreased from the northern to the central highlands. Overall, 148 indigenous tree, shrub and liana species were recorded across the 78 surveyed forests. Patch α-diversity increased with mean annual precipitation, but typically only 25 woody species occurred per patch. The combined results showed that >50% of tree species present in tropical northeast Africa were still present in the 78 studied church forests, even though individual forests were small and relatively species-poor. Tree species composition of church forests varied with elevation and precipitation, and resembled the potential natural vegetation. With a wide distribution over the landscape, these church forests have high conservation value. However, long-term conservation of biodiversity of individual patches and evolutionary potential of species may be threatened by isolation, small sizes of tree species populations and disturbance, especially when considering climate change. Forest management interventions are essential and should be supported by environmental education and other forms of public engagement.


Key words: Africa; forest fragments; landscape ecology; relic vegetation; remote sensing; sacred groves

1. **Introduction**

Sacred groves are community-preserved, often small, forest patches in which certain spiritual, cultural or religious values contribute to the conservation of biodiversity and ecosystem services (Berkes 2009; Dudley et al. 2009; Ray et al. 2014). Sacred groves may be remnants of earlier more continuous forests or planted or regenerated forest patches in non-forest landscapes (Bhagwat et al. 2014). Because sacred groves are usually protected by local institutions or by-laws that regulate resource use (Kibet 2011), such sites are often better protected than other small habitat patches, and can therefore play an intrinsic role in biodiversity conservation (Ceperley et al. 2010; Metcalfe et al. 2010; Rutte 2011; Daye and Healey 2015). Traditionally, conservation efforts have focused either on large and relatively undisturbed habitats because large areas conserve relatively more species (Laurance 2005), or on biodiversity hotspots with exceptional concentrations of endemic species under relatively high levels of threat (Myers et al. 2000). However, conserving a number of small habitat patches such as sacred groves can have additional value for conserving biodiversity, for instance by covering a wider variety of habitats than would be achieved by protecting a few large patches of an equivalent total area (Bhagwat and Rutte 2006; Hokkanen et al. 2009) and thus contributing to higher total biodiversity covered (Benedick et al. 2006). Another important benefit is that a habitat network enabling dispersal amongst sacred groves and other protected areas (Laita et al. 2010; Chiarucci et al. 2012) may make an important contribution to genetic connectivity (Lander et al. 2010) and the survival of species as metapopulations (sensu Hanski 1998). In particular when it is not feasible to maintain large tracts of pristine habitat, for instance because the landscape is intensively used as cropland after extensive past deforestation (Arroyo-Rodríguez et al. 2009), the conservation and restoration of small habitat patches, such as sacred groves, may turn out to be the final safety net to conserve a high proportion of the landscape's previous biodiversity (Fischer and Lindenmayer 2002).

Sacred groves exist in many countries (for reviews see Bhagwat and Rutte 2006; Dudley et al. 2010), and there are well documented examples throughout Asia (e.g. Brandt et al. 2013; Gao et al. 2013; Gunaga et al. 2013; Allendorf et al. 2014) and Africa (e.g. Mgumia and Oba 2003; Campbell 2004; Sheridan and Nyamweru 2007; Kokou et al. 2008; Tankou et al. 2014). In the highlands of northern and central Ethiopia, sacred groves associated with Ethiopian Orthodox Tewahedo churches and monasteries (EOTC) are known as 'church forests'. These church forests are virtually all that is left of the Ethiopian Afromontane forest (Aerts et al. 2006; Wassie et al. 2010; Berhane et al. 2013; Jacob et al. 2014) (Fig. 1 and Fig. S1-S4) and local people rely on these church forests for the provisioning of livestock feed, tree seedlings, fuelwood, honey, clean water and other essential ecosystem services including shade, climate regulation, habitat for pollinators and spiritual values (Cardelús et al. 2012; Amare et al. 2016). In the southwest of the country, shade coffee cultivation has, until now, guaranteed that more or less natural forest remained an important land cover (Tadesse et al. 2014), despite the clear trade-off between coffee productivity and forest ecological quality (Senbeta and Denich 2006; Schmitt et al. 2010; Aerts et al. 2011; Hundera et al. 2013). In the central and northern Ethiopian highlands, however, high historical land use pressure has resulted in widespread deforestation and land degradation (Darbyshire et al. 2003; Nyssen et al. 2004). Crop land and degraded grazing land are the dominant land covers, with only very few patches of forest remaining and these are almost entirely confined to the vicinity of churches, monasteries and other holy sites such as springs. Churches manage their forests autonomously, and management varies from strict protection (with some churches surrounded by walls and patrolled by paid forest guards) to weak protection with poorly controlled harvesting of trees (Amare et al. 2016). A number of studies has evaluated the conservation value of these church forests at local scales (e.g. Aerts et al. 2006; Wassie et al. 2010;

Berhane et al. 2013) but, to date, there is no information on the contribution of church forests to the conservation of biodiversity and ecosystem services at the larger scale, i.e. the entire Ethiopian highlands. This information is, however, urgently needed to enable the integration of these habitat patches into wider (global) conservation strategies (Dudley et al. 2009) and to understand what actions must be undertaken to conserve these forests, which are known for their exceptionally high vertebrate and plant diversity, rich in narrow-range species (Burgess et al. 2006).
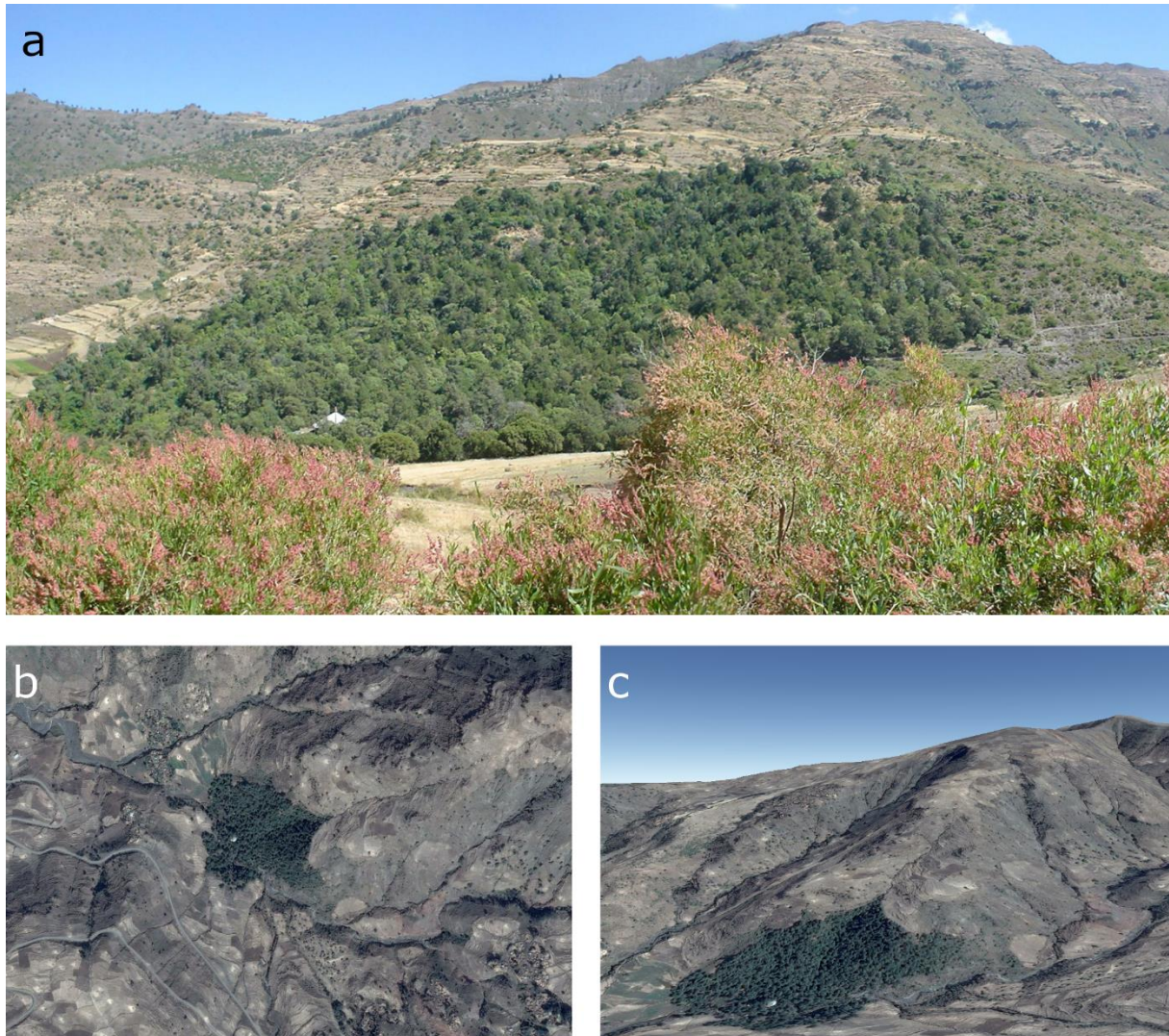
Fig. 1. Church forest C794 in the central highlands of Ethiopia (12° 24.0'N 39° 2.6'E):

(a) Photograph (panorama of 2 images) by Raf Aerts (16.11.2006); (b) Overhead and (c) oblique VHR satellite imagery over a global DTM in Google Earth. Satellite image © 2014 CNES/Astrium by way of Google Earth. Eye altitude in (b) 5 km, average patch diameter 363 m. The observed sharp delineation of the patch in the VHR satellite image corresponds to a true sharp forest edge in the field.

The spatial arrangement and patch characteristics of church forests are important because the viability of a population within a habitat fragment or patch depends, among other factors, on the number of patches, the size of the individual patches, the isolation of the patches and the edge effects associated with the shapes of the patches (Fahrig 2003). An understanding of what woody plant communities are conserved in church forests is important because their conservation value at the regional scale depends on the species and communities that persist in the church forests and on how well these communities relate to the potential

natural vegetation of the region. Therefore, our main research questions were the following: How do the number of church forests, their isolation, their shape and their size vary throughout the northern and central Ethiopian highlands? What are the woody species and plant communities that are conserved in the church forests? Does environmental variation contribute to differences in woody plant diversity and community composition in church forests? To that end, we (1) perform the first large-scale spatially-explicit assessment of church forests, combining remote-sensing data and the largest dataset based on field studies of church forests to date, (2) determine the woody plant communities conserved in church forests and relate diversity of church forests to environmental variables, (3) identify the main challenges to biodiversity conservation in church forests, and (4) present guidelines for management and policy to maintain and improve the forests' ecological and environmental quality and health.

2. Methods

2.1. Study area

The Ethiopian highlands consist of a region of elevated plateaus and mountain ranges with elevations over 1600 m above sea level which rise abruptly from the surrounding plains (Fig. 2a). The northern and central highlands, lying approximately between 10° and 15° N, are marked by deeply incised river valleys, the large Tana Lake that forms the source of the Abay or Blue Nile, and the Simien Mountains that peak at 4533 m on Mount Ras Dashen. These highlands extend between the lowlands at the southwestern shore of the Red Sea in the north, the Danakil depression and the Ethiopian Rift Valley in the east and the valley of the Upper Nile in the west.

Nyssen et al. (2004; 2014) provided an extensive overview of the environment of the Ethiopian highlands. The climate varies with elevation, but on the plateaus rainfall is generally bimodal, with a short and erratic February-April rainy season and a long and intensive June-September rainy season. Precipitation generally increases from east to west and from north to south, yielding a mean annual precipitation of 600 mm in the northeast to more than 2000 mm in the southwest (of the northern and central highlands). Soils vary with elevation and parent material (mainly sandstone, limestone and volcanic rock) and include Cambisols over limestone and Leptosols and Vertisols over shallower or more clayey parent material, respectively..
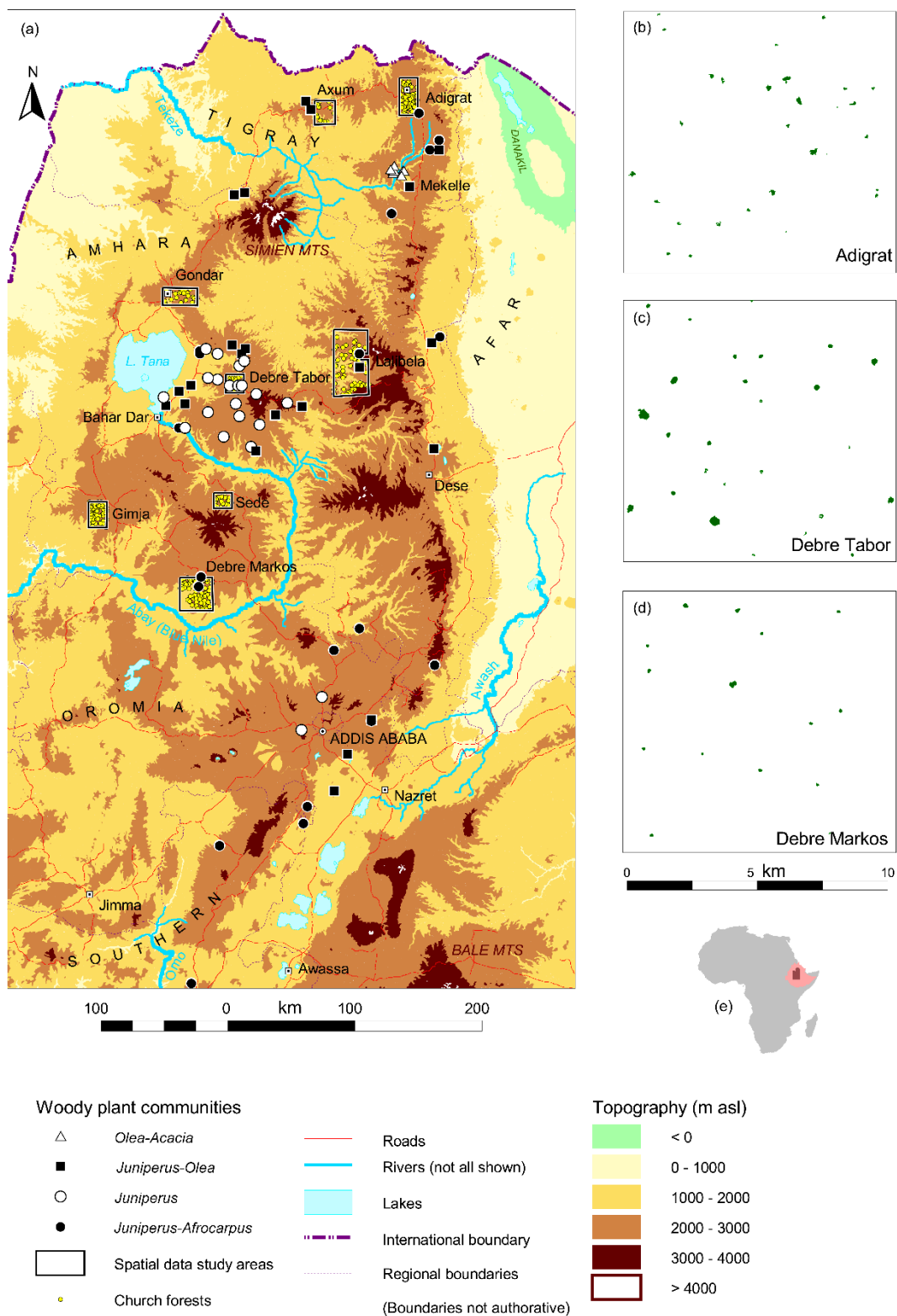
Fig. 2. Location of the sampled church forests in the highlands of northern and central Ethiopia (a) and location of the study area in Ethiopia and Africa (e). The 78 church forests sampled in the floristic survey are labeled with circles, triangles or squares to show their woody species community of the four floristically-defined groups produced by cluster and indicator species analysis (a). The larger rectangles show the location of the eight areas used for spatial data analysis; church forests are shown as small yellow circles. To illustrate the distribution of church forests in the landscape, inset maps show church forests for three 10×10 km^2 windows within the Adigrat (b), Debre Tabor (c) and Debre Markos (d) areas.

Pollen records indicate the prevalence of the Afromontane forest tree species *Afrocarpus falcatus* (earlier known as *Podocarpus falcatus*), *Juniperus procera* and *Hagenia abyssinica* in the landscape prior to anthropogenic disturbance (Darbyshire et al. 2003). The potential natural vegetation (PNV), sensu Friis et al. (2010), of the highlands between 1800 and 3000 m altitude is the 'dry evergreen Afromontane forest and grassland complex' (DAF) in areas with rainfall below 1700 mm·year^{-1} and 'moist evergreen Afromontane forest' (MAF) in areas where rainfall exceeds 1700 mm·year^{-1}. The DAF is a complex system comprising a variety of forest and woodland types, from grasslands with shrubs and trees to closed-canopy forest. Different subtypes of this forest are marked by differences in dominance of the indigenous coniferous species *A. falcatus* and *J. procera* and/or in the relative abundances of grass, shrubs or broadleaved trees present in the forest. One subtype of the DAF is the 'undifferentiated Afromontane forest', which is 'either *Juniperus-Afrocarpus* forest or tends towards single-species dominant *Afrocarpus* or *Juniperus* forest, both with an element of broad-leaved species' (Demissew et al. 2004). Another subtype of the DAF is the 'dry single-species dominant Afromontane forest of the Ethiopian highlands' in which 'the typical dominant species in the upper storey is *Juniperus,* with *Olea europaea* subsp. *cuspidata* and a number of other species below' (Demissew et al. 2004). The MAF, also known as Afromontane rainforest, has *A. falcatus* and *Pouteria adolfi-friederici* as diagnostic highland species (and, notably, no *J. procera*) and gradually changes into transitional rainforest at elevations below 1500 m (Demissew et al. 2004).

Land use in the highlands is dominated by small-scale, rain-fed agriculture, within a landscape mosaic of cropland and degraded shrub land used for livestock grazing and browsing, with sparsely distributed woodlots of planted exotic tree species (generally *Eucalyptus* and *Cupressus* species; Teketay et al. 2010), church forests, livestock grazing exclosures with recovering shrub and tree vegetation, few isolated remnant trees and wooded gullies providing tree resources in the landscape.

2.2. Remote sensing data collection and analysis

A two-stage sampling design was used for studying the population of church forests that occupy the northern and central highlands of Ethiopia (> 1600 m above sea level). In the course of the year 2010, we screened the highlands in Google Earth (GE) for very high resolution (VHR) imagery (minimum pixel resolution 0.8 m) (see Fig. S1, Fig. S3) and selected eight blocks located between 36° 49' E – 39° 33' E and 10° 00' N – 14° 22' N (first stage), covering a total area of 440 879 ha (Fig. 2a). The eight blocks were randomly selected among a larger set of candidate areas spanning a wide geographical range over the highlands. Within these blocks, all church forests were identified and digitized by systematically scanning the images visually on-screen (i.e. by means of human, visual interpretation of the images, not by automatic polygon detection) (second stage). Forest fragment perimeters and the locations of buildings (church or monastery) within each fragment were digitized (Fig. S5).

Spatial data were then analyzed using Patch Analyst 3.1 (R. Rempel, http://www.cnfer.on.ca/SEP/patchanalyst/) and a nearest-feature extension (Jenness Enterprises, http://www.jennessent.com/arcview/nearest_features.htm) implemented in ArcView GIS 3.2 (ESRI, Redlands, CA). For each fragment we calculated patch properties that were expected to be related to patch biodiversity (see Fahrig 2003): patch size (ha) (a measure of habitat size, with larger habitats expected to be more diverse), perimeter (m), perimeter:area ratio (m ha^{-1}), Patton shape index SI, fractal dimension FD (with higher values

of these measures indicating potentially stronger edge effects and negative consequences for forest specialist species), distance to the nearest and second-nearest neighboring fragment (measures of isolation, with increasing isolation expected to have negative consequences for the fitness of plant populations and ultimately on species diversity) and the distance between the church and the center of the fragment (a measure that differentiates between simple, round patches with a central building and more complex forest shapes, potentially related to the genesis of these forests). We defined forest 'core area' as the central section of the forest patch where edge effects are presumed to be absent by subtracting an inward buffer of 50 m (with 50 m > three average tree heights, the buffer dimension generally used to determine forest edge area; Harris 1984). The steep slopes in the highlands mean that strong meteorological differences can exist between north- and south-facing slopes, with south-facing slopes receiving more solar insolation, potentially increasing local heat and water stress. We therefore used a 200-m digital terrain model from the EthioGIS geospatial data compilation (CDE, 1999) to determine slope angle and slope aspect θ, which we transformed to a relative measure for heat load (HL, higher values indicate higher heat and water stress) using the equation $HL = [1-\cos(\theta)]/2$ (McCune and Keon 2002). The patch variables were correlated with forest fragment coordinates to detect geographic variation in patch characteristics.

The average number of church forests per 1000 ha and the average patch size of the church forests were used to estimate the total number of church forests throughout the Ethiopian highlands and the total forest cover conserved in these church forests.

2.3. Vegetation data collection and analysis

Original vegetation data were obtained from five different field studies covering a total of 78 unique sites (Fig 1a): Aerts et al. (2006), 10 forests, 31 20×20m plots; Aynekulu et al. (2012), 1 forest, 29 50×50m plots; TewoldeBerhan (2003), 1 forest, 16 10×10m plots; Teklehaimanot et al. (2004), 38 forests, plotless inventory data; Wassie et al. (2010), 28 forests, 810 10×10m plots. The main criteria for including forest patches in the sampling strategy used across the studies included accessibility, permission and local knowledge of forest presence. From the pool of available forests, individual studies sampled forests to encompass different patch sizes and different local environments based on random sampling after local stratification. The vegetation data were used to construct species lists of woody plants (trees, shrubs and lianas, including *Dracaena* species and palms but excluding exotic species because we focus on conservation of indigenous vegetation). Because differences in plot sizes potentially led to differences in species richness as the probability of finding additional species increases with increasing plot size, we aggregated data to fragment level to produce a single list of the species recorded as present for each church forest. With this conversion, information about species' relative abundances was lost, but it minimized the potential bias caused by the species-area relationship and enabled calculation of reliable floristic distance measures across studies. Any differences found amongst forests are consequently caused by differences in species composition, not abundance. The final dataset contained presence/absence information of 148 indigenous tree, shrub and liana species for 78 forests.

Geographic location (coordinates north and east, elevation), site environment variables (mean annual precipitation, distance to nearest river, slope and aspect transformed into heat load) and indices of human impact (distances to nearest road and nearest town, total urban and rural population of nearest town) were recorded for each forest through overlay and nearest feature operations on the EthioGIS (CDE, Bern) datasets in ArcView GIS. The map of the

potential natural vegetation of Ethiopia (Friis et al. 2010) was used to compare church forest vegetation to potential natural vegetation zones. Patch alpha diversity was correlated with forest fragment coordinates and environmental variables using Spearman rank correlation.

For the classification of the woody plant communities in the sampled church forests, an indirect gradient approach was adopted. To identify plant communities, church forests were clustered into $k = 2$–6 groups using a Sørensen distance measurement and flexible beta linkage ($\beta = -0.25$) (McCune and Mefford 1999). To identify the most informative number of plant communities (clusters), we used Indicator Species Analysis (Dufrêne and Legendre 1997) and calculated indicator values for all N species, their individual significance P_i and the overall mean significance $\Sigma P_i/N$ for each of the k cluster steps. The first cluster step where the overall mean significance reached a local minimum was considered the most informative. Homogeneity within groups was tested with a multiresponse permutation procedure (MRPP) test. For MRPP, we used the Sørensen distance measure and a natural group weighting factor $n_i/\sum n_i$ (where n_i is the number of samples in each group). In MRPP, the test statistic T describes the separation between groups and the chance-corrected within-group agreement A describes within-group homogeneity compared to a random expectation. If the emerging groups are significantly more homogeneous than expected by chance, then $1 > A > 0$ (McCune and Mefford, 1999). Nonmetric multidimensional scaling (NMDS) based on the Sørensen distance measure was used to investigate the gradients potentially influencing species distribution. NMDS was run using starting coordinates from a preliminary solution, two final dimensions, 250 iterations, an instability criterion of 10^{-5} and a rotation for maximum variance (McCune and Mefford 1999). To interpret the NMDS axes, which are linear combinations of plant species but expected to reflect environmental gradients, Spearman rank correlation coefficients were calculated between the NMDS scores obtained and the recorded environmental variables. Correlations were evaluated after Bonferroni correction for multiple tests.

Relative frequencies of species within communities were used to construct rank-frequency curves, which give information on the relative frequency and diversity within communities. Steep curves indicate that few species have a wide distribution (few species present in many samples) and that species composition varies considerably between samples (high beta diversity: many species present in only a few samples). Less steep curves indicate higher evenness between samples (more species present in many samples). To evaluate the spatial distribution of plant communities, we tested our dataset for isolation by distance, i.e. for a Mantel correlation between pairwise Sørensen dissimilarity indices and pairwise geographical distances.

Classification, ordination and statistical tests were conducted using PC-ORD 5.0 for Windows (MjM Software, Gleneden Beach, OR). All other statistical analyses were performed in SPSS 15.0 for Windows (SPSS Inc., Chicago, IL). The nomenclature follows the Flora of Ethiopia and Eritrea, Vol. 1-8 (1989-2009).

3. Results

3.1. Spatial distribution and patch characteristics of church forests

A total of 402 church forests were identified in the 0.44×10^6 ha area of land surveyed using remote sensing (Fig. 2). Of these forests, 394 were located in the dry evergreen Afromontane forest and grassland complex zone (DAF; 1800-3000 m, annual precipitation < 1700 mm yr^{-1}), which was the focus of the study. Five forests were located in higher elevation zones – three in the ericaceous belt (3000-3200 m) and two in the afro-alpine belt (> 3200 m). Three forests were located near the lower limit of the DAF in the *Combretum-Terminalia* woodland and wooded grassland zone.

Within the DAF zone ($N = 394$ forests sampled), the forests were consistently small with remarkably similar surface area (mean and SE mean: 2.48 ± 0.24 ha) and on average separated by 1.92 ± 0.06 km from the nearest neighboring church forest (Table 1; Fig. S3). Church forests were sparsely distributed, with on average (over all inventoried study blocks) only 0.99 ± 0.18 forests per 1000 ha (10 km²). Based on an internal buffer of 50 m, only 149 fragments (38%) had a forest core area, with an average size of 1.32 ± 0.29 ha.

The perimeter-area ratio, shape index and fractal dimension of the church forests decreased towards the west and towards the south, indicating a gradient of decreasing shape complexity, but not size, from NE to SW (Fig 1b–d). Along the same gradient, the terrain slope became less steep, and the position of the church within the forest fragment changed from a position near the edge (Fig. S2) towards a more central position (Fig. S4) (Table 2).

Table 1

Patch characteristics of church forests in the dry evergreen Afromontane forest and grassland complex zone of the northern and central highlands of Ethiopia, sampled by remote sensing ($N = 394$).

	Mean	SE mean
Area (ha)	2.48	0.24
Perimeter (m)	737	37
Perimeter:area ratio (m m^{-2})	0.055	0.002
Patton shape index	1.512	0.026
Patch fractal dimension	1.351	0.002
Distance to nearest neighboring patch (m)	1923	58
Distance to second nearest neighboring patch (m)	2766	70
Distance between church and patch centroid (m)	48	4

Table 2

Geographical variation of patch characteristics of church forests in the dry evergreen Afromontane forest and grassland complex zone in the northern and central highlands of Ethiopia ($N = 394$).

|	west to east		south to north	
	R	p	R	p
Area	0.087	0.085	0.028	0.580
Perimeter	0.122	0.016	0.093	0.064
Perimeter:area ratio	**0.191**	**< 0.001***	**0.298**	**< 0.001***
Patton shape index	**0.222**	**< 0.001***	**0.327**	**<0.001***
Patch fractal dimension	**0.275**	**< 0.001***	**0.398**	**< 0.001***
Distance to nearest neighboring patch	0.046	0.362	–0.130	0.010
Distance to second nearest neighboring patch	0.141	0.005	–0.050	0.324
Distance between church and patch centroid	**0.201**	**< 0.001***	**0.188**	**< 0.001***
Slope	**0.362**	**< 0.001***	**0.190**	**< 0.001***
Heat load	**–0.312**	**< 0.001***	–0.109	0.030

* Significant correlation. Pearson's correlation coefficients R between patch metrics and patch coordinates in UTM 37N (X = west to east; Y = south to north) need to be evaluated against a corrected $\alpha_{corr} = 0.005$ to assure an overall significance of $\alpha = 0.05$ (Bonferroni correction for ten tests).

3.2. Woody plant communities in church forests

In the 78 ground-surveyed church forests, the most widespread tree species (relative frequency $f_r > 0.5$ in 78 forests) were *Olea europaea* ssp. *cuspidata* ($f_r = 0.71$), *Juniperus procera* ($f_r = 0.67$) and *Croton macrostachyus* ($f_r = 0.54$). *Calpurnia aurea* and *Carissa spinarum* (both $f_r = 0.76$) were the most common shrub species. On average, there were 24.6 woody species per forest patch (α diversity; 16.9% of the sampled species pool). For the 148 indigenous tree, shrub and liana species recorded across the 78 forests, each species occurred on average in 17% of the forests. Patch alpha diversity increased with increasing mean annual precipitation ($r_s = 0.486$, $p < 0.001$), a gradient overlapping a geographical gradient from northeast to southwest (north: $r_s = -0.477$, $p < 0.001$; east $r_s = -0.480$, $p < 0.001$). Species dissimilarity between the forest fragments was high (overall mean Sørensen dissimilarity 71%; similarity 29%). The dissimilarity was strongly related to geographical distance between fragments, indicating a strong isolation-by-distance effect (Mantel $t = 7.307$, $p < 0.001$).

Clustering the sample plots in four floristically-defined groups provided the most informative solution with respect to plant communities (Table 3; Table S1). The separation between groups and homogeneity within objective clusters were higher than could be expected by chance (MRPP T= –28.13; A = 0.15; p < 0.001). Two plant communities belonged to the dry single-species-dominant Afromontane forest of the Ethiopian highlands. The first community was a degraded subtype which could be called *Olea* forest with *Acacia* and drought-resistant shrubs (*Olea-Acacia*) (10 forests, in total 30 species, 1779-2362 m elevation range in our sample); the second community was typical dry Afromontane forest

dominated by *Juniperus* with *Olea* and other species as secondary species (*Juniperus-Olea*) (22 forests, 109 species, 1490-2980 m). The two other plant communities were classified as undifferentiated Afromontane forest: one community represented a subtype with *Juniperus* as single-dominant species, mixed with broadleaved elements (*Juniperus*) (21 forests, 113 species, 1816-3111 m); the other community was the more typical undifferentiated forest with both *Juniperus* and *Afrocarpus*, mixed with broadleaved elements (*Juniperus-Afrocarpus*) (23 forests, 107 species, 1650-2700 m). The *Olea-Acacia* forest had the least species. Both the *Olea-Acacia* and the *Juniperus-Olea* forests had a low evenness of species. The undifferentiated Afromontane *Juniperus* and *Juniperus-Afrocarpus* forests had more species and a higher evenness (Fig. 3).
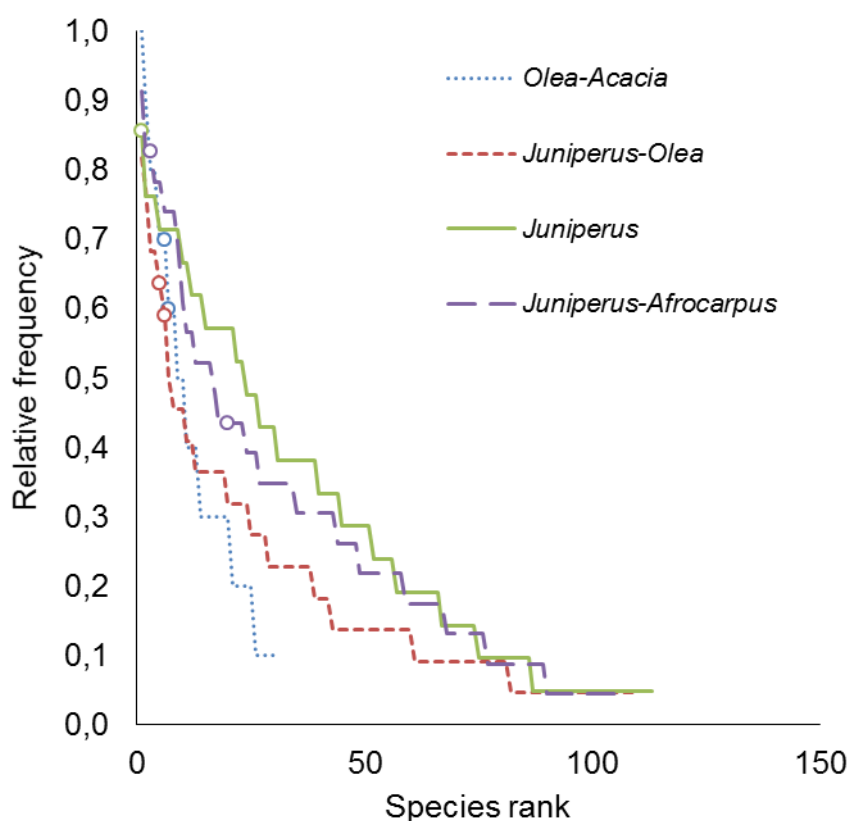
Fig. 3. Dominance-diversity curves of four floristically-defined woody species communities determined by cluster and indicator species analysis of 78 church forests in Ethiopia. Steep curves indicate dominance (as measured by relative frequency) by relatively few species; curve length along the horizontal axis is directly related to community γ-diversity (total species richness). Circles indicate the positions of the species used in the names of the communities.

Table 3

Woody species communities of 78 surveyed church forests in the dry evergreen Afromontane forest and grassland complex zone of the northern and central highlands of Ethiopia produced by cluster and indicator species analysis. For each community, the ten most frequent woody species are listed with their relative frequency. Frequencies for the Afromontane conifers are also given in the bottom two rows where they are not in the ten most frequent species.

Dry single-species-dominant Afromontane forest				Undifferentiated Afromontane forest			
Olea-Acacia (N=10)		*Juniperus-Olea* (N=22)		*Juniperus* (N=21)		*Juniperus-Afrocarpus* (N=23)	
Euclea racemosa [S]	1.00	*Calpurnia aurea* [S]	0.82	**Juniperus procera** [T]	0.86	**Bersama abyssinica** [T]	0.91
Rhus natalensis [S]	0.90	*Carissa spinarum* [S]	0.77	**Osyris quadripartita** [S]	0.76	**Dovyalis abyssinica** [T]	0.83
Calpurnia aurea [S]	0.80	*Croton macrosachyus* [T]	0.68	**Buddleya polystachya** [T]	0.76	*Juniperus procera* [T]	0.83
Carissa spinarum [S]	0.80	*Olea europaea* [T]	0.68	**Euphorbia abyssinica** [T]	0.76	*Calpurnia aurea* [S]	0.78
Cassia sp. [S]	0.70	*Juniperus procera* [T]	0.63	*Carissa spinarum* [S]	0.71	*Carissa spinarum* [S]	0.78
Olea europaea [T]	0.70	**Dodonaea angustifolia** [S]	0.59	**Vernonia myriantha** [S]	0.71	**Vernonia auriculifera** [S]	0.74
Acacia abyssinica [T]	0.60	*Grewia ferruginea* [T]	0.50	**Clausenia anisata** [T]	0.71	**Ekebergia capensis** [T]	0.74
Acokanthera schimperi [T]	0.60	*Pterolobium stellatum* [S]	0.45	**Maytenus arbutifolia** [T]	0.71	*Olea europaea* [T]	0.74
Leucas abyssinica [S]	0.50	*Rhus glutinosa* [S]	0.45	*Olea europaea* [T]	0.71	**Allophylus abyssinicus** [T]	0.70
Teclea nobilis [S]	0.50	*Cordia africana* [T]	0.45	*Calpuria aurea* [S]	0.67	*Croton macrostachyus* [T]	0.61
Juniperus procera [T]	0						
Afrocarpus falcatus [T]	0	*Afrocarpus falcatus* [T]	0.09	*Afrocarpus falcatus* [T]	0.14	**Afrocarpus falcatus** [T]	0.43

The relative frequencies are frequencies within the communities (ranging between 0 and 1). Superscripts indicate life forms: trees (T) and shrubs (S) – no liana species were in the ten most frequent species in any of the four communities. Species in bold are significant (p<0.05) indicator species for that community. See Table S1 for a complete list of indicator species, indicator values and significances.

Community names are based on the most prominent species, not necessarily the strongest indicator species.

In the NMDS ordination (cumulative $R^2 = 0.643$), degraded *Olea-Acacia* and *Juniperus-Olea* forests were partitioned from the other dry Afromontane forests along the first dimension (38.0% of variance explained), which represented a geographical gradient (northeast to southwest), coinciding with a gradient of increasing rainfall, increasing urban and rural population and decreasing distance to towns (Fig. 4; Table S2). The second

dimension (26.3% of variance explained) represented an altitudinal gradient of increasing elevation (Fig. 4; Table S2).
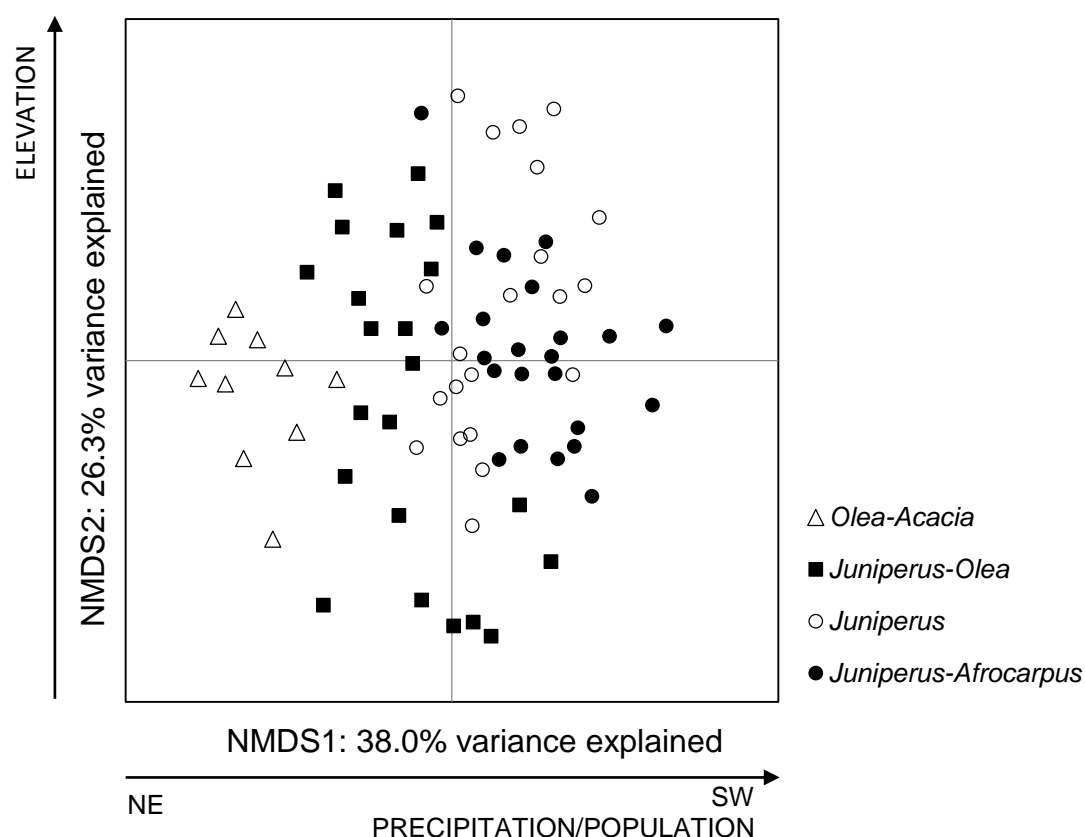
Fig. 4. Ordination of 78 church forests in the northern and central highlands of Ethiopia based on nonmetric multidimensional scaling (NMDS) of tree and shrub species occurrence. Forests are labeled according to woody species communities produced by cluster and indicator species analysis. The mean annual precipitation gradient in our sample ranges between 550 and 1950 mm; the elevation gradient between 1490 and 3111 m above sea level.

4. Discussion

4.1. Remote sensing data reveal numerous small, isolated forests

The remote sensing data revealed that individual church forests were typically small with little or no forest core area free from edge effects. The complexity of the forest shapes decreased from NE to SW. More regularly shaped patches are usually related to lower negative edge effects and increased core habitat quality (Fahrig 2003), but the less complex (i.e. round) forests featured more centrally located churches and were located in more densely populated areas and this obviously also negatively affects core habitat ecological quality (Fig. S4).

The nearest neighbor distance between patches was ~2 km but the patch density was only one forest per 1000 ha. This indicates that the patch distribution is not entirely uniform, as in a perfectly organized grid a nearest neighbor distance of 2 km would yield a patch density of one forest per 400 ha. Given a total area of 19.4×10^6 ha potentially covered by

DAF (Friis et al. 2010) and a density of ~1 forest fragment per 1000 ha, and assuming that there is no bias in the location of the eight surveyed areas, the estimated number of church forests throughout the Ethiopian highlands potentially covered by DAF is 19 400. This is probably a conservative estimate, as a government report mentions a total of 35 000 churches throughout the highlands (IBC 2012). The extrapolated total cover of forest estimated to be conserved in our estimated 19 400 church forests (95% confidence interval, not including other forest remnants) throughout the Ethiopian highlands is ~39 000-57 000 ha. This total amounts to merely 0.20-0.30% of the land that could potentially be covered by DAF. In comparison, an estimated total of 102 000 ha of high forest exists throughout Amhara and Tigray regions, the two main regions of the studied highlands (WBISPP 2004). Throughout Ethiopia, an estimated 4 million ha of high forest persists to date, but the vast majority of these forests (3.9 million ha) are moist forests in the southwestern regions of the country (WBISPP 2004). Church forests thus contribute to regional conservation of DAF, not by conserving a large amount of habitat (the cumulative habitat area is rather small, especially when compared with the moist forests), but rather by conserving a large number of patches, well distributed throughout the region, and covering the widest possible range of environmental conditions.

4.2. Field survey data reveal high floristic variability

The vegetation in the sampled church forests could be classified into four plant communities which are phases of the DAF that vary with rainfall and geographical gradients. Nevertheless, species dissimilarities or beta species diversity amongst individual church forests were high. Individual species occurred on average in only 13 out of the 78 sampled forest patches . Similar and even lower occurences of tree species have been found in other sets of small tropical forest fragments, for instance in tropical rainforest fragments in Los Tuxtlas, Mexico, where 41% of the recorded species occurred in only one or two patches (Arroyo-Rodriguez et al. 2009), and in rainforest patches in Chiapas, Mexico, that shared on average only 27% of species (Hernandez-Ruedas et al. 2014). Individual forests were also rather species-poor, each containing on average only 25 species of woody plants or 16.9% of the sampled species pool. Nevertheless, a total of 148 indigenous woody species were observed in all patches combined, which is more than half of the ca. 270 tree species that occur in tropical northeast Africa (Friis 1992) and which is more than the numbers of woody species that are reported for the few contiguous natural forests left in the region (e.g. 43 woody species in Menagesha forest and 66 woody species in Hugumburda forest, both *Juniperus-Olea* forest with some scattered *Afrocarpus*) (Demissew 1988; Aynekulu 2011). These results highlight that Ethiopian church forests, much like other sacred forest sites in the world (Bhagwat and Rutte 2006), are important for regional forest biodiversity conservation, but also that there is a need for a region-wide conservation strategy for the church forests of the Ethiopian highlands.

As plant communities varied with rainfall and geography, the large species differences between fragments and thus high beta diversity and high species turnover in the region are most likely related to environmental variation. Dissimilarities in plant species composition could, however, also be partially attributed to differences in species extinctions between fragments as some woody species may be more susceptible than others to the detrimental effects of small population sizes in the small and isolated forests. It is known that a small population size negatively affects population genetic diversity and especially in outcrossing species (Honnay and Jacquemyn 2007; Aguilar et al. 2008). Small fragments can indeed only support small populations, and small populations are susceptible to inbreeding and random genetic drift, resulting in poor adaptive potential to changing environmental conditions,

reduced fitness and increased probabilities of extinction (Keller and Waller 2002). Increasing shape complexity and associated deleterious edge effects may further increase the vulnerability to local extinction, in particular for forest specialist species (Murcia 1995; Bender et al. 1998; Ewers and Didham 2006). As habitat quality deteriorates through loss of woody plants in forest fragments, local extinctions of other taxa such as birds can be expected, for instance through loss of keystone species (Cordeiro et al. 2015) or increased niche competition (Visco et al. 2015). Even when species persist in forest fragments, their genetic diversity may not, and hence the long term viability of their populations may be at risk (Struebig et al. 2011). Under these circumstances the degree of functional isolation of fragments is particularly important: if dispersal amongst fragments occurs sufficiently frequently then species and their genetic diversity can survive in such habitat networks as meta-populations, despite a high rate of local extinction in individual fragments (Hanski 1998). Exchange of plant genetic material between isolated forest fragments can occur via pollen flow and via seed dispersal. Habitat fragmentation limits pollen flow of woody species, even in wind-pollinated species, hampering the replenishment of alleles that may have been lost through genetic drift in the small populations (Vranckx et al. 2012). If mating events occur mainly within fragments, between neighboring and possibly related trees, this may increase the risk of inbreeding and induce lower fitness in future generations (Vranckx et al. 2014). Although birds, including large and small frugivores such as hornbills and thrushes, are relatively well conserved in the church forests (Aerts et al. 2008), and although the regionwide establishment of grazing exclosures during the previous decades may have provided stepping stones and an improved landscape connectivity for seed vectors (Aerts et al. 2008), it is unclear to what extent these birds act as effective seed dispersal vectors. Also, if mating patterns are mainly local and offspring therefore potentially inbred, seed dispersal may have a limited genetic rescue effect and therefore it remains unclear if birds reduce functional forest isolation at all. Overall, the evolutionary potential of the woody species in the church forests can be expected to be low, jeopardizing adaptation of the populations to emerging pests and diseases such as outbreaks of *Corynelia,* a fungal pathogen of *Afrocarpus falcatus* (Assefa et al. 2014), or to changing environmental conditions such as climate change

4.3. Combined data suggest historical legacies of past human activities

The plant communities observed in the church forests sampled throughout the northern and central highlands of Ethiopia belonged to the dry evergreen montane forest and grassland complex and represented different spatial phases of the potential natural vegetation of the area. A geographical northeast to southwest gradient and differences in elevation separated dry single-species-dominant Afromontane forest communities (degraded *Olea-Acacia* forest and *Juniperus-Olea* forest) from richer undifferentiated Afromontane forest communities (*Juniperus* and *Juniperus-Afrocarpus* forests with broadleaved elements). The underlying driver of this distinction is most likely the increase in annual rainfall along this gradient (Table S2), with the western highlands wetter than the eastern (Crummey 2000). Higher precipitation was marked by an increase in importance of the indigenous conifers, in particular *A. falcatus*, and of species more typical of mesic or moist site conditions such as *Albizia gummifera* and *Coffea arabica*. In particular coffee is not an element of the potential natural vegetation, but has been planted into church forests. Also *Cupressus lusitanica*, *Citrus* spp., *Eucalyptus* spp., *Grevillea robusta*, *Jacaranda mimosifolia*, *Melia azedarach* and *Pinus* spp.that that were recorded in the studied forests. These species exotic to Ethiopia are commonly planted in church forests (and plantations) for their specific use values. Such species improve the benefits for local users, but may also contribute to the degradation of the natural forest by replacing indigenous trees and shrubs (Amare et al. 2016).

Other differences in past forest use may also have contributed to the differentiation between the relatively species-poor *Olea-Acacia* and *Juniperus-Olea* forests and the other, richer communities. High-value timber species such as *J. procera* and *A. falcatus* may have become locally extinct in some intensively used patches but not in others, as also noted in fragmented Afromontane forests elsewhere (Thijs et al. 2014). In the *Olea-Acacia* community forests (in the northeast of the study area), the prevalence of drought-tolerant, early-successional shrub species such as *Euclea racemosa*, *Rhus natalensis* and *Calpurnia aurea* (Table 3), and the absence of *J. procera* and *A. falcatus*, do suggest degradation (Aerts et al. 2006). In the *Olea-Acacia* community, removal of the original canopy trees (presumably *J. procera*) may have resulted in harsher microclimatic conditions, rendering these forests more similar to vegetation types of drier sites at lower elevations, such as *Acacia-Commiphora* woodland. Other research in the region has shown that such degradation is still ongoing, with logging, fires and tree dieback of *J. procera* and *O. europaea* ssp. *cuspidata* causing community shifts from dry Afromontane forest to shrubland (Aynekulu et al. 2011).

Historical land use pressures may also have had an impact on forest species composition. Owing to high land-use pressure and widespread conversion of natural habitat to agricultural land in the northeastern highlands around 500 BC (Darbyshire et al. 2003), churches that were established in that region much later may have been placed near already isolated and degraded forest patches in a largely deforested landscape. Present-day trees may even stem from relatively recent regrowth, as evidenced by the comparison of historical and recent landscape and aerial photographs of that region (Nyssen et al. 2009; 2016). The round shape, the central position of the church, the low standard deviation of mean distance between forest patches and the spatial arrangement of churches and forests (Fig. S3, S4, S6) in the central highlands might, on the contrary, suggest systematic planning of church establishment in a landscape with more intact forest, for instance as a component of strategies to control the land (Crummey 2000). The landscape pattern of church forests is sometimes remarkably similar to a von Thünen landscape with regularly spaced markets, or to orderly spaced towns in settlement-distribution theories (see e.g. Ullman 1941). Fig. S6The structure and composition of contemporary church forest vegetation may thus primarily be a product of environmental variables and human factors, as elsewhere in Eastern Africa (Bongers and Tennigkeit 2010), but differences between forests could be enhanced by random species losses, and legacies of historical land use and institutional strategy. Future archaeological, anthropological and socio-ecological research using, among other approaches, participatory resource inventories and socio-economic surveys would provide more information on how individual decisions and group-level institutional decisions may have shaped the church forest plant communities.

5. Implications for forest conservation management and policy

5.1. Improve policy to conserve forests more efficiently

The high floristic dissimilarities amongst individual church forests and the small population sizes mean there is little redundancy. To maintain species diversity and associated ecosystem services, a high proportion of patches needs to be conserved (see also Hernandez-Ruedas et al. 2014). This is because low frequencies of species entail high extinction risks when patches are lost, and because extinction risks are high in landscapes with low vegetation cover, low connectivity, degraded vegetation and intensive land use in the matrix (Fischer and Lindenmayer 2007).

The survival to date of so many church forests in Ethiopia is a testament to the historical and contemporary importance of the cultural, spiritual and religious values with which they are associated. Nevertheless, given that both historical and present land use rights, and religious and governmental laws apply, the legal conservation status of these forests is an extremely complex matter. Uncertainties in boundary and land ownership issues complicate conservation, especially along the edges of the forests. Providing legislative instruments that strengthen conservation and management of forests by the church and other community-based groups could strengthen Ethiopia's forest conservation strategy. These policies should aim to strengthen, not replace, local forms of forest protection (Brandt et al. 2015; Denier et al. 2015).

5.2. Manage forests to improve forest quality and stakeholder benefits

Not only must the number of church forests be maintained, but also the patch quality. Ideally patch quality should be improved, as in other areas where little forest remains (Turner and Corlett 1996). Locally, future management of church forests should be focused on ensuring ecological sustainability, including its synergy with the sustaining of cultural values. Rather than excluding human activities, the relevant institutions should focus on management and restoration measures that ensure the favorable conservation status of the DAF habitats and species while at the same time increasing involvement of and benefits for local communities (Amente et al. 2010; Denier et al. 2015; Amare et al. 2016). To that end, forest management should focus on (i) avoiding further encroachment and reducing unfavorable edge effects, for instance by boundary demarcation and participatory management with surrounding land users; and (ii) avoiding further internal degradation of the forest by controlling grazing, browsing and tree cutting (Wassie et al. 2009a,b).

Increasing tree cover in a surrounding buffer zone through locally appropriate agroforestry practices, including DAF tree species present in the church forests, can contribute to local livelihoods and assist in conserving biodiversity within the forest (Teketay et al. 2010; Amare et al. 2016). This would enable the development and conservation of an expanded or new forest core area within the existing boundary of the church forest. In this way the functional ecological area of the church forest would be enlarged, thus reducing the extinction risks for tree populations, without harming the livelihoods of local people dependent on this land. Spatially targeted expansion of such buffer zones and establishment of new forest patches within the matrix located at distances compatible with dispersal distances of trees may play an important role in increasing the quality of the matrix (see e.g. Lemenih and Bongers 2010; Telila et al. 2015), thereby decreasing the functional isolation of species' populations within a network of forest patches and reducing the risks of extinction (Vandermeer and Carvajal 2001; Berens et al. 2014).

Management within the existing church forest areas should focus on ensuring healthy populations of tree species. This could be accomplished by assisting natural regeneration of extant species (in the first place by excluding livestock), and by planting nursery raised seedlings or direct seeding of species missing from that patch, thus improving their distribution among the patches (see e.g. Wassie et al. 2009a,b). A number of PNV distribution models based on edaphic factors and projected climate conditions, with or without projected fire frequency distributions in the year 2070, predict a widespread replacement of DAF by *Combretum-Terminalia* woodland and, to a lesser extent, by MAF in the current southern range of the DAF (van Breugel et al. 2015). Active forest management should therefore take account of current and future environmental changes and make strategic choices of species to regenerate to climate-proof the biodiversity of the church forests.

Finally, and very importantly, forest management has to be supported by environmental education (Keane et al. 2011), community-based monitoring (Dickinson et al. 2012) and other forms of public engagement required for conservation planning for multiple stakeholders (Githiru and Lens 2007; Denier et al. 2015). These may be supported by payment for ecosystem services schemes (Petheram and Campbell 2010; Amare et al. 2016; Deng et al. 2016; but see Poudyal et al. 2016). Without active involvement of all stakeholders, illegal forest use including grazing and logging will remain critical issues.

5.3. Seek international recognition for Ethiopia's church forests

Despite the conservation issues discussed above, the Ethiopian church forests are of outstanding universal value. This is essential for them to be included on UNESCO's World Heritage List, for which they must meet at least one out of ten selection criteria (http://whc.unesco.org/en/criteria/). The Ethiopian church forests do not meet only one but a staggering six criteria to qualify as mixed religious, natural and cultural heritage, i.e. criterion (iii), to bear a unique or at least exceptional testimony to a cultural tradition which is living; criterion (v), to be an outstanding example of human settlement and land-use which is representative of a culture, or a human interaction with the environment especially when it has become vulnerable under the impact of irreversible change; criterion (vi), to be directly associated with living traditions or with beliefs; criterion (vii), to contain areas of exceptional natural beauty; criterion (ix), to be an outstanding example representing significant on-going ecological and biological processes in the evolution and development of terrestrial ecosystems and communities of plants and animals; and criterion (x), to contain the most important and significant natural habitats for *in situ* conservation of biological diversity, including those containing threatened species of outstanding universal value from the point of view of conservation.

The inclusion of the church forests in the Tentative List of Ethiopian natural and cultural heritage sites (http://whc.unesco.org/en/statesparties/et) and, ultimately, its inscription on UNESCO's World Heritage List would provide timely and well-deserved recognition of the exceptional religious, natural and cultural value of Ethiopia's church forests. The management and policy issues of Ethiopian church forests have global relevance, because small and isolated forest patches and woodlots are becoming increasingly important as global deforestation and forest fragmentation continue.

Acknowledgements

Electronic supplementary material

Satellite images and other supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.scitotenv.2016.02.034.

Glossary

DAF   dry evergreen Afromontane forest

MAF   moist evergreen Afromontane forest

PNV   potential natural vegetation

VHR   very high resolution satellite imagery

NMDS   non-metric multi-dimensional scaling

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SUPPLEMENTARY MATERIAL

Conservation of the Ethiopian church forests: threats, opportunities and implications for their management

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Fig. S1 Typical landscape in the northern highlands of Ethiopia

Fig. S2 Church forest C249 in the northern highlands of Ethiopia

Fig. S3 Typical landscape in the central highlands of Ethiopia

Fig. S4 Church forest C578 in the central highlands of Ethiopia

Fig. S5 Church forest digitization process

Fig. S6 Deforestation frontier in the central highlands of Ethiopia

Table S1 Indicator species for woody species communities of church forests

Table S2 Spearman rank correlations between NMDS scores and environmental variables

Fig. S1 Typical landscape in the northern highlands of Ethiopia (14° 0.8'N 38° 46.1'E). Image © 2014 CNES/Astrium by way of Google Earth. Eye altitude 10 km, surface area approximately 9×5 km².

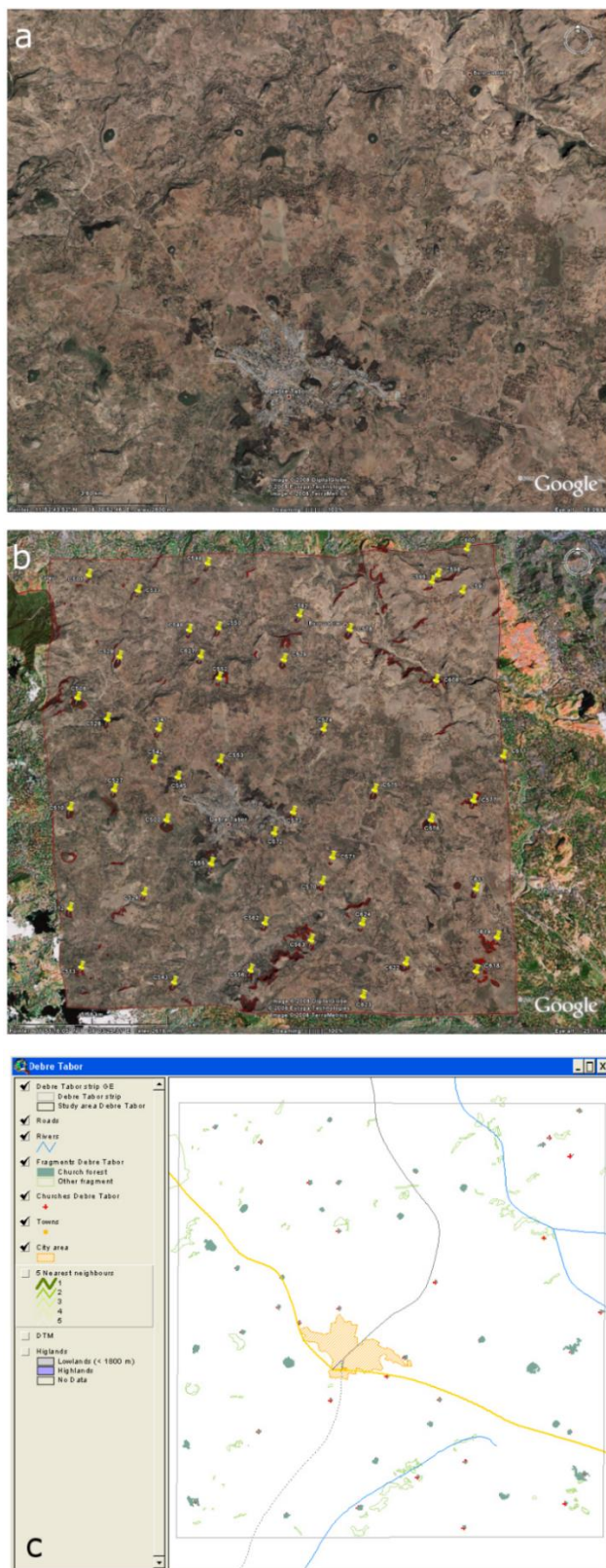**Fig. S2** Church forest C249 in the northern highlands of Ethiopia (14° 0.8'N 38° 46.1'E), located in the center of Fig. S1. Image © 2014 CNES/Astrium by way of Google Earth. Eye altitude 3 km, distance from church to southern edge 370 m. Note irregular shape and highly variable forest quality within the patch.

Fig. S3 Typical landscape in the central highlands of Ethiopia (11° 54.8'N 38° 3.0'E). Image © 2014 CNES/Astrium by way of Google Earth. Eye altitude 10 km, surface area approximately 9×5 km². The average distance between the three church forests on the left of the image is 2.1 km.

Fig. S4 Church forest C578 in the central highlands of Ethiopia (11° 54.8'N 38° 3.0'E) located in the center of Fig. S3. Image © 2014 CNES/Astrium by way of Google Earth. Eye altitude 3 km, patch radius 120 m. Note regular shape, central location of the church and almost uniform quality throughout the patch.

Fig. S5 High spatial resolution images in Google Earth (a) were digitized on screen (b) and via KML format imported into ArcView GIS (c). Digitized boundaries are not part of the Google Earth source material but an interpretation of the authors and therefore do not inherit any copyright from the source material.

Fig. S6 Deforestation frontier in the central highlands of Ethiopia (10° 50.9'N 36° 33.6'E). Image © 2014 CNES/Astrium by way of Google Earth. Eye altitude 15 km, east-west extent ~17 km, image date 03/01/2014. In the deforested landscape in the southern half of the image forest vegetation only persists in church forests, while in the northern half larger blocks of forest are still present (image date 03/01/2014). Note the almost grid-like pattern of church forests in the south and the process of isolation ongoing in the upper left corner of the image.

Table S1

Indicator species for woody species communities of church forests in the dry evergreen Afromontane forest and grassland complex zone of Ethiopia produced by cluster and indicator species analysis.

Dry single-dominant Afromontane forest				Undifferentiated Afromontane forest			
Olea-Acacia (*N*=10)		*Juniperus-Olea* (*N*=22)		*Juniperus* (*N*=21)		*Juniperus-Afrocarpus* (*N*=23)	
Rhus natalensis[S]	86 (<0.001)	*Cordia africana*[T]	25 (0.015)	*Vernonia myriantha*[S]	67 (<0.001)	*Vernonia auriculifera*[S]	66 (<0.001)
Euclea racemosa[S]	50 (<0.001)	*Dodonaea sp.*[S]	25 (0.05)	*Urera hypselodendron*[S]	57 (<0.001)	*Allophylus abyssinicus*[T]	55 (<0.001)
Cassia sp.[S]	50 (<0.001)	*Ficus vasta*[T]	23 (0.039)	*Osyris sp.*[S]	45 (<0.001)	*Bersama abyssinica*[T]	51 (<0.001)
Psiadia punctulata[T]	30 (<0.001)	*Rydingia integrifolia*[S]	19 (0.036)	*Canthium oligocarpum*[S]	45 (<0.001)	*Dovyalis abyssinica*[T]	46 (<0.001)
Combretum collinum[T]	30 (<0.001)	*Acacia polyacantha*[T]	19 (0.042)	*Clausena anisata*[T]	41 (<0.001)	*Jasminum stans*[S]	44 (<0.001)
Leucas sp.[S]	28 (<0.001)	*Rhus pyroides*[S]	18 (0.026)	*Buddleja polystachya*[T]	40 (0.001)	*Euphorbia candelabrum*[T]	37 (<0.001)
Faidherbia albida[T]	26 (<0.001)			*Euphorbia abyssinica*[T]	38 (0.001)	*Ekebergia capensis*[T]	37 (0.002)
Acacia seyal[T]	14 (0.044)			*Dombeya torrida*[T]	36 (<0.001)	*Pavetta spp.*[S]	34 (0.002)
				Rosa abyssinica[S]	35 (0.004)	*Maytenus obscura*[T]	32 (0.002)
				Maytenus arbutifolia[T]	35 (0.009)	*Maytenus gracilipes*[T]	31 (0.002)
				Schrebera alata[T]	34 (0.001)	*Vepris nobilis*[S]	28 (0.004)
				Juniperus procera[T]	32 (0.020)	*Afrocarpus falcatus*[T]	28 (0.005)
				Albizia schimperiana[T]	31 (0.003)	*Vernonia leopoldii*[S]	27 (0.003)
				Schefflera abyssinica[T]	30 (0.001)	*Blumea elatior*[S]	27 (0.009)
				Erythrina brucei[T]	28 (0.006)	*Brucea antidysenterica*[T]	27 (0.022)

Ritchiea albersii[S]	28 (0.005)	*Maesa lanceolata*[S]	25 (0.015)
Teclea nobilis[S]	28 (0.014)	*Ficus sur*[T]	24 (0.018)
Rhus glutinosa[S]	28 (0.023)	*Discopodium penninervium*[S]	24 (0.018)
Syzygium guineense[T]	25 (0.004)	*Galiniera saxifraga*[S]	23 (0.020)
Hypericum revolutum[T]	24 (0.002)	*Euphorbia depauperata*[T]	22 (0.019)
Combretum molle[T]	22 (0.012)	*Albizia gummifera*[T]	22 (0.019)
Rhus vulgaris[S]	22 (0.016)	*Rubus steudneri*[S]	22 (0.020)
Millettia ferruginea[T]	21 (0.042)	*Rytigynia neglecta*[S]	22 (0.022)
Ficus ovata[T]	19 (0.028)	*Dracaena afromontana*[T]	18 (0.043)
		Maytenus undata[T]	17 (0.042)

The indicator values range from zero (no indication) to 100 (perfect indication). *p*-values (in parantheses) are calculated from a Monte Carlo permutation test for each species. Superscripts indicate life forms: trees

(T) and shrubs (S). Only species with a significant indicator value ($p < 0.05$) are shown.

Table S2

Spearman rank correlations between NMDS scores and environmental variables for church forests in the dry evergreen Afromontane forest and grassland complex zone of Ethiopia ($N = 76$).

	NMDS1 ($R^2 = 0.380$)		NMDS2 ($R^2 = 0.263$)	
	R_S	p	R_S	p
Degrees north	-0.568	< 0.001*	0.058	0.617
Degrees east	-0.465	< 0.001*	0.382	0.001*
Elevation	0.294	0.010	0.679	< 0.001*
Mean annual precipitation	0.638	< 0.001*	0.080	0.494
Distance to rivers	0.203	0.079	0.036	0.755
Distance to roads	-0.063	0.586	0.196	0.089
Distance to towns	-0.416	< 0.001*	0.022	0.847
Urban and rural population	0.380	0.001*	-0.016	0.888
Slope	-0.061	0.603	0.171	0.139
Heat load	0.070	0.549	0.160	0.893

*Spearman rank correlation coefficients R_S between NMDS scores and environmental variables need to be evaluated against a corrected $\alpha_{corr} = 0.005$ to assure an overall significance of $\alpha = 0.05$ (Bonferroni correction for ten tests).