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Sacred natural sites as mensurative fragmentation experiments in long-inhabited multifunctional landscapes

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Well-controlled landscape experiments have played key roles in advancing fragmentation science, but such experiments are costly and may not be possible in many ecosystems – including the long-inhabited landscapes typical of many developing countries. In such contexts observational studies of pre-existing forest patches may offer valuable insights, but these bring other challenges including the non-random location of patches, the heterogeneous matrix between patches, and patch-specific management practices that may influence forest community composition. This paper argues that sacred natural sites might provide a middle ground between experimental and observational studies, allowing for more rigorous mensurative fragmentation experiments in long-inhabited multi-functional landscapes. To illustrate this potential, we analyze the drivers of productivity in 'church forests' across northern Ethiopia. These forest patches conserved by followers of the Ethiopian Orthodox church provide ample variation in area, edge, and surrounding matrix characteristics. Church forests also provide variation in long-term forest community composition, elevation and rainfall. Finally, unlike most observational studies, church forests offer a relatively stable institutional structure, including longstanding religious norms, allowing researchers to control for some heterogeneity in human influences. By combining remotely sensed data on church forest patches (n = 2558) with field data on church forest tree species composition (n = 27) and social survey data on church forest management practices (n = 145 respondents in 6 church communities) we show how ecological and anthropogenic factors influence church forest productivity. Like experimental patches, church forest productivity increases with size and decreases with amount of edge; productivity also increases with rainfall and increased tree species diversity within a given patch. But there is also evidence that church forest productivity and species composition are both affected by human management rooted in longstanding religious norms. Findings highlight how studies in sacred natural sites systems might help understand relationships between forest productivity, species diversity, and human management in long-fragmented landscapes.

Large-scale landscape fragmentation experiments – which seek to isolate the effects of habitat loss and fragmentation on ecological communities while controlling for various abiotic, biotic, and anthropogenic influences – have played a key role in identifying the negative consequences of fragmentation for species diversity and ecosystem function (Fayle et al. 2015, Haddad et al. 2015). Well-controlled experiments can effectively isolate components of fragmentation such as patch area, edge effects or connectivity, controlling for quality of the surrounding matrix (e.g. Kansas fragmentation experiment, Holt et al. 1995), amount of edge and connectivity (e.g. corridor experiment, Tewksbury et al. 2002), while holding relatively constant less controllable factors such as land use history and socio-cultural context (Debinski and Holt 2001, Tollefson 2013). But while these are powerful 'whole system' experiments that allow for replication, their spatial scale remains necessarily limited. By design landscape experiments are large-scale, resource-intensive, and long-term (Debinski and Holt 2001), making them physically unfeasible, logistically difficult or cost-prohibitive in many regions, including key biodiversity hotspots – which disproportionately occur in low-income or war-torn countries where pressures on land are great and land tenure insecure (Hanson et al. 2009, Kramer et al. 2009). Yet such landscapes are arguably where the conservation implications of fragmentation research are most relevant.

In contexts where controlled fragmentation experiments are not possible, existing fragments of remnant forest may provide an opportunity – and sometimes the only opportunity – to study the natural history of unique, diminishing ecosystems. Observational studies that take advantage of existing remnant fragments in working landscapes have provided powerful examples of the net effects of fragmentation in the face of heterogeneous ongoing land uses (Flinn and

Velland 2005, Laurance 2008, Driscoll et al. 2013, Ripperger et al. 2015, Comte et al. 2016). But pre-existing fragments present their own challenges for ecological research, including the non-random location of remnants (e.g. often on relatively less arable sites as opposed to more fertile, flat tillable land, Flinn and Velland 2005), and the heterogeneous matrix between remnants (Laurance 2008, Driscoll et al. 2013, Brudvig et al. 2017). Observational studies are especially limited by their inability to control for known sources of confounding variability in multi-functional production landscapes (Lovell and Johnston 2009, O'Farrell and Anderson 2010), including past and ongoing human management practices ranging from fuelwood collection to livestock grazing, to selective conservation of high value fruit trees, medicinal trees, and timber species – that over time can substantially influence community composition (Brook et al. 2008, Haddad et al. 2014, Comte et al. 2016).

Recognizing the limitations of past observational studies has led some researchers to call for more rigorous 'mensurative' studies of existing fragments, i.e. study designs across multiple pre-existing fragments allowing researchers to partially control for at least some variation where experimental manipulation is not possible (McGarigal and Cushman 2002). But while theoretically feasible, in practice access to well-replicated pre-existing patches is rare. Access to large numbers of patches with similar habitat amounts but varying configurations is uncommon, especially for any given matrix type (Gobeil and Villard 2002, Villard and Metzger 2014). This has constrained the ability of researchers to design and implement mensurative fragmentation experiments at the landscape scale (McGarigal and Cushman 2002, Robichaud et al. 2002), with few examples in developing country contexts (Prist et al. 2012).

In this paper, we argue that sacred natural sites offer a unique opportunity to study fundamental and applied ecological questions relating to habitat loss and fragmentation in under-studied, heavily disturbed landscapes. Forest patches conserved around places of worship can be found in the midst of otherwise cleared land in many low-income countries, and often in large numbers. In Ghana there are over 1400 sacred forests (Bossart and Antwi 2016), in Tanzania over 600 sacred groves, in India over 100 000 sacred forests, and in Japan Shinto and Buddhist shrine forests cover over 110 000 hectares (Castro and Brokensha 1990, Bhagwat and Rutte 2006, Nahendra and Gokhale 2008, Verschuuren et al. 2010). At the local level these diverse sites play important roles in religious and traditional beliefs and practices, ranging from strict preservation (e.g. holy forest sites only rarely entered or used), to more intensively managed sacred forest systems which may include permanent habitation by priests or monks, community prayer spaces for regular services or holidays, or extraction of wood, food, medicinal plants, holy water, and other forest resources (Verschuuren et al. 2010). At the regional and global levels networks of geographically dispersed sacred natural sites can also serve as key refugia for plant and animal species (Mgumia and Oba 2003, Dudley et al. 2009, Bossart and Antwi 2016), increase water filtration, mitigate soil erosion, and provide an array of other ecosystem services (Daily 1997, Millennium Ecosystem Assessment 2005, Bodin et al. 2006, Hernández-Morcillo et al. 2013, LoTemplio et al. 2016). The biodiversity of sacred natural sites has already begun to attract international attention (Wild et al. 2008, Verschuuren et al. 2010), and some ecologists now advocate prioritization of sacred natural sites for preservation (Shen et al. 2012).

We expand the small but growing body of ecological scholarship on sacred natural sites through a case study showing how sacred natural sites might offer an effective middle ground between experimental and observational fragmentation studies, potentially allowing for more rigorous mensurative studies of the consequences of habitat loss and fragmentation in long-cleared, mixed agricultural systems. As an illustration of this potential, we examine the ecological and social drivers of forest composition and productivity – key variables of interest in fragmentation theory (Cardinale et al. 2011, 2012, Collins et al. 2017, Thompson et al. 2017) – in longstanding patches of dry Afromontane forest conserved by followers of the Ethiopian Orthodox Tewahido Church.

One of the oldest Christian churches in Africa, the Ethiopian Orthodox Church has a long history of protecting and preserving native forest as sanctuaries for prayer (Wassie 2002, Bongers et al. 2006). Today church forests can be found across northern Ethiopia in great numbers – there are reportedly more than 35 000 Orthodox communities (Wassie et al. 2010), with recent estimates based on satellite imagery placing the likely number of church forests in these communities at roughly 19 400 (Aerts et al. 2016). In addition to their large numbers, church forests offer great variation along key attributes of interest to fragmentation research including area, edge, isolation, and forest productivity – allowing researchers to statistically control for these factors to a much greater degree than is possible in most observational studies (Fig. 1).

Church forests also vary in several important attributes less easily manipulated through fragmentation experiments; for example their broad geographic extent provides variation in abiotic factors (elevation, rainfall) as well as difficult-to-control landscape characteristics such as surrounding matrix quality. Additionally, church forests provide variation in forest community composition, including patches comprised of diverse, old-aged native tree species (Wassie et al. 2010). These characteristics potentially allow for church forests to serve as the foundation for relatively rigorous mensurative research testing hypotheses surrounding the long-term effects of habitat loss and fragmentation – including current debates around the consequences of species loss for ecosystem function (i.e. diversity–productivity relationships) (Cardinale et al. 2011) – across a variety of ecological gradients. Finally, unlike most observational or experimental studies, church forests also offer a relatively stable and identifiable institutional structure (Ostrom 1990, 2005, 2010), including longstanding religious norms shaping preferences around forest uses and management (Bongers et al. 2006, Tilahun et al. 2015). This, combined with the longevity and minimal disturbance of church forests – even in heavily degraded landscapes (Scull et al. 2016) – allows researchers to control for at least some heterogeneity in past and ongoing human influences that might affect forest species composition, productivity, or both.



		Existing Patches		Church Forests		Landscape Experiments	
		Range of Conditions	*Potential for Mensurative Research*	*Range of Conditions*	*Potential for Mensurative Research*	*Range of Conditions*	*Potential for Mensurative Research*
Patch Attributes	Area	Moderate	Low	Moderate +	Moderate	Moderate	High
	Edge : Area	High	Low	High	Moderate	High	High
	Isolation	High	Low	Moderate	Moderate	Moderate	Moderate
	Productivity	High	Low	High	Moderate	Low	Low
Landscape Context	Elevation	High	Low	High	High	Low	Low
	Rainfall	High	Low	High	Moderate	Low	Low
	Matrix quality	High	Low	Moderate +	High	Low	Low
Socio-cultural context	Patch Age	High	Low	High	Moderate	Low	Low
	Human population	High	Low	High	High	Low	Low
	Historical land use	High	Low	Low	Moderate	Low	Low
	Current management	High	Low	Low +	Moderate	High	High

Figure 1. Ethiopian Orthodox church forests provide intermediate possibilities on the spectrum of non-experimental to experimental approaches to fragmentation research. For each aspect of fragmentation research (rows), remnant forests not associated with churches, church forests, and landscape experiments (columns) are roughly categorized (high, moderate, low) according to the range of environmental conditions typically offered within the scope of a single study, and the degree to which fragment attributes may be manipulated or statistically controlled to isolate aspects of fragmentation experimentally.

We first draw upon a large sample of 2558 church forests across three adjacent administrative zones in northern Ethiopia to explore the drivers of forest productivity in Ethiopian Orthodox church forests across a variety of patch attributes including area, edge, and isolation (Haddad et al. 2017, Resasco et al. 2017), controlling for various abiotic factors (elevation, rainfall), biotic factors (surrounding matrix composition), and anthropogenic factors (human population, livestock density, market access). We then explore the question of whether forest productivity in church forests might be positively influenced by woody species diversity (Ruiz-Jaen and Potvin 2010, Maurer and McGill 2011), combining remotely-sensed data with detailed field data on species composition and abundance collected from 27 forests spanning a range of abiotic, biotic, and anthropogenic gradients. Finally, we draw upon social surveys in six church forest communities to consider how local knowledge surrounding the ecological and management history of sacred natural sites might both improve our interpretation of ecological patterns (including species abundance distributions within and across church forests) as well as allow for further empirical testing of hypotheses about human impacts on forest composition and productivity alike. Findings suggest sacred natural sites may offer not only the potential for relatively rigorous mensurative forest fragmentation research in otherwise under-studied landscapes, but also an opportunity to better understand the impacts of socio-cultural influences on species diversity and forest productivity – through the combination of ecological and social science research methods in contexts where ecological variation across patches can be great, while socio-cultural variation remains relatively small.

Methods

Landscape-level data on Ethiopian Orthodox Tewahido church forests

We build upon an original spatial dataset with the locations of over 8500 church forests in the Amhara Peoples National Regional State (Amhara Region) of northern Ethiopia (Fig. 2, Reynolds et al. 2015).

Using high-resolution Google Earth satellite imagery we digitized the perimeter of 2558 church forests following standardized criteria including: 1) the 'core' of each forest patch was considered to include the main church building (typically at the center) and any native trees or groups of trees within 100 m; 2) the outer perimeter of each church forest included all contiguous forest cover as well as native trees or groups of trees within a 10 m distance of the core forest, and excluded any trees outside a 10 m distance; 3)

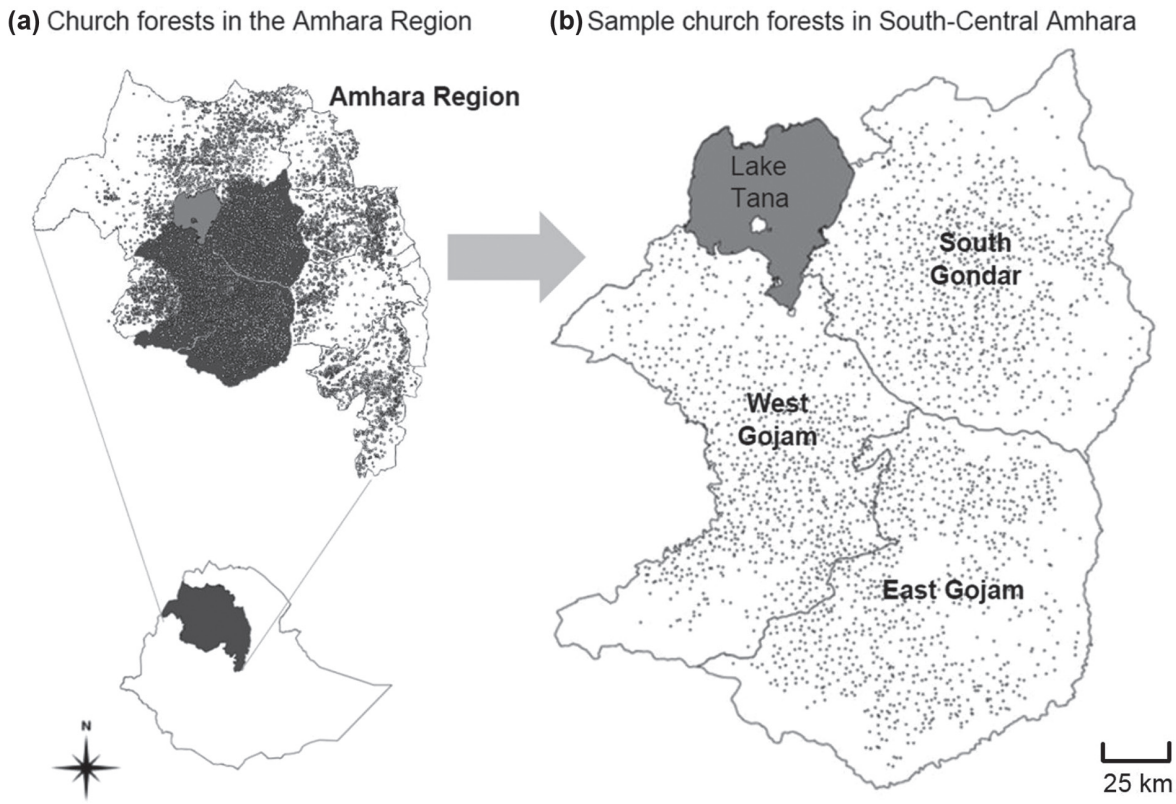


Figure 2. (a) Church forests in Amhara Region, Ethiopia. Using high-resolution satellite imagery, Reynolds et al. (2015) catalogued over 8500 identifiable church forests ranging from < 1 ha to over 100 ha distributed across the 254 710 km² Amhara Peoples National Regional State of northern Ethiopia. Church forests can be found at virtually every latitude, longitude and elevation, and embedded in every agro-ecology in the region. (b) Our sample of 2558 church forests. Sampled forests are located in South Gondar, West Gojam, and East Gojam Administrative Zones.

the outer perimeter of each church forest included plantation species that were contiguous with the church forest's native vegetation (primarily *Eucalytpus globulus* and *Eucalyptus camaldulensis* in the study area; Liang et al. 2016) but excluded non-tree crops; and 4) in rare cases where the outer perimeter of a church forest was not clear, or where scattered trees continued over a large area, two or more coders independently estimated the perimeter and a consensus estimate was used.

We then used 30 m resolution data from the USGS Landsat 8 satellite (USGS 2015) to calculate the Normalized Difference Vegetation Index (NDVI), an index of the green biomass of a landscape (Huete et al. 2002, Pettorelli et al. 2005, Martinuzzi et al. 2008), for each church forest and the surrounding agricultural land (Fig. 3). Plants absorb energy in the red area of the electromagnetic spectrum (RED) while reflecting energy in the near-infrared (NIR); NDVI combines these characteristics into a single index

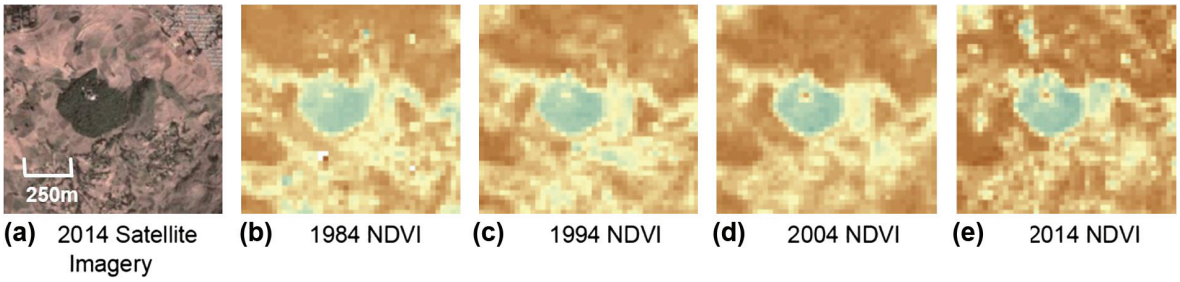


Figure 3. Example of church forest size and vegetation density at Debresena Mariam church in South Gondar, Ethiopia. (a) Google Earth imagery used to digitize current church forest perimeter. (b)–(e) Normalized Difference Vegetation Index (NDVI) from 1984–2014 based on 30 × 30 m USGS Landsat satellite data; vegetation density was calculated for each church forest and the surrounding matrix (mean NDVI of a 500 m buffer surrounding each forest). The maps show relative stability of the forest fragment size over the past 30 years (consistent with findings by Scull et al. 2016). Maps do reveal some vegetation loss since 1984 along the northeastern edge of the forest, as well as expansion of the clearing at the center of the forest since 1994. We also see the introduction of *Eucalyptus* spp. in the matrix north and east of the church forest since 2004.

(NDVI = (NIR – RED)/(NIR + RED)) which can range from –1 to 1 with values closer to 1 indicating high green vegetation content. The use of NDVI as a proxy for land productivity is supported by multiple rigorous studies that have identified a strong relationship between NDVI and net primary productivity (NPP) (summarized in Yengoh et al. 2015). We processed all Landsat scenes into regional 30 m resolution NDVI raster datasets using R v3.2.2. Data were obtained for January (short rainy season), April (dry season), July (early rainy season), and October (late rainy season) for 2014–2015 to examine inter-seasonal variation in church forest vegetation cover.

Because elevation and rainfall influence forest diversity and productivity (Gentry 1988, Ruiz-Jaen and Potvin 2010, Ricklefs and He 2016) we drew upon elevation data from the Aster 30 m digital elevation model (DEM) and 2014 monthly rainfall data from the Famine Early Warning System (FEWS NET 2014). Additional NDVI data were used to measure variation in vegetation cover in the surrounding matrix (Fig. 3). These include intra-annual cropping vegetation patterns and variation in permanent vegetation cover, with high dry season NDVI values in the matrix typically indicating the presence of exotic tree plantations (*Eucalyptus* spp.) on nearby farmland (Liang et al. 2016). Finally, to further account for the potential influence of human-induced stresses in determining forest productivity, we considered socioeconomic and livelihood variables including population density (hypothesized to increase demand for forest resources and potentially weaken local forest governance institutions; Ostrom 2005) and livestock density per square kilometer (expected to decrease forest productivity via grazing pressures; Wassie et al. 2009) and distance to market (expected to decrease productivity through increasing reliance on forests for fuelwood and timber). Spatial data for these variables were obtained from the International Food Policy Research Institute's HarvestChoice database (HarvestChoice 2015).

Church forests species composition and abundance

Detailed species composition and abundance data were collected from field surveys of 27 forests spanning a range of sizes and geographic locations. The sample forests vary in areas from 1.6 ha to 100 ha, and are located at altitudes ranging from 1816 m to 3111 m a.s.l. The 27 forests fall in two agro-climatic zones, *Woyna-Dega* (1500–2300 m) and *Dega* (2300–3200 m). In each forest, 10×10 m plots were established at 100 m intervals along transects. The number of transects, and hence plots, varied with forest size. In total 168 different woody species were identified (summarized in Wassie et al. 2010). To account for greater sampling effort in larger forests, species richness data were rarified to seven plots, the minimum number of plots sampled in any forest. Additional site characteristics and sampling are described in detail in Wassie et al. (2010) (Supplementary material Appendix 1).

Socio-cultural context

Finally, we administered a socio-economic survey to a randomly selected sample of 145 households across six church forest villages during the long rainy season (July–August) in 2015. Church forests in the sample were selected to control for known variation in species present along an elevation gradient (Wassie et al. 2010), including 1) two high-elevation forests, 2) two medium-elevation forests, and 3) two low-elevation forests. Interviewees were household heads (typically male) or spouses, and all were members of the church under study. Each interview lasted 30–45 min and was conducted by a trained local enumerator. Most interviews took place inside or just outside the interviewee's home; all were within a short walk – and often within sight – of the respondent's church forest. Interviews consisted of 67 questions ranging from demographic information to in-depth attitudinal questions relating to church forest uses and management. We focus on a subset of questions on perceptions of the ecosystem services provided by various tree species in the church forest. Each respondent was first asked the open-ended question "What trees should be planted in the church forest?" and the first five tree species mentioned were recorded. Respondents were then asked a series of closed-form questions about the ecosystem services provided by 12 prominent native tree species, including yes/no questions about eight possible species benefits ranging from shade to provision of construction wood (Supplementary material Appendix 2).

Analysis

Although the multitude of environmental and anthropogenic factors influencing forest productivity are not strictly controlled in Ethiopian Orthodox church forests, in such large networks of patches impressive replication exists for the forest attributes most manipulated by scientists (Fig. 4). Patch characteristics routinely studied, manipulated, or controlled for in landscape-scale fragmentation research include size, proportion of edge, and isolation (Debinski and Holt 2001, Haddad et al. 2015). Bivariate relationships between these variables and productivity in church forests appear consistent with findings from experimental fragmentation studies – with increasing productivity with increasing patch size and decreasing productivity with greater edge and isolation (Fig. 4a–c).

To further examine the overall drivers of church forest productivity we first conducted a series of multiple linear regression models using the lm() procedure in R with church forest size, edge:area ratio, and vegetation productivity (using NDVI as a proxy) as dependent variables, considering the relative contributions of the environmental and social variables in Fig. 4 as predictors. Since spatial autocorrelation in the model residuals might lead to bias in coefficient estimates, we calculated the Moran's I statistic for each regression model (lm.morantest() in R) using a neighborhood approach based on all neighboring church forests within 25 km. Where present, spatial autocorrelation was addressed using a simultaneous autoregressive (SAR) model, with a Lagrange multiplier test employed to select the most appropriate model for the data among alternative SAR options (Dormann et al. 2007).

Next, to explore whether church forest species diversity might positively influence forest productivity (as

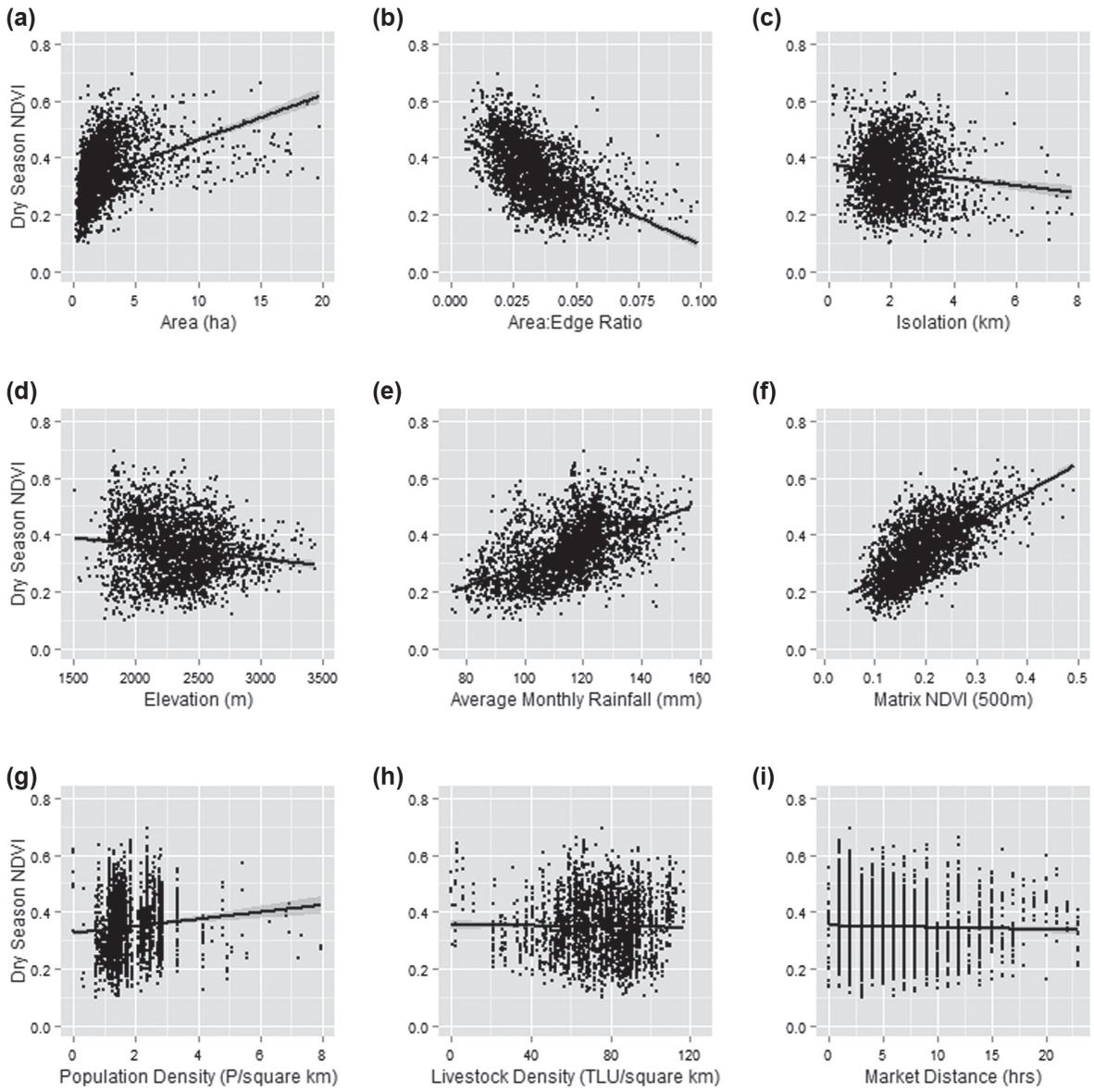


Figure 4. Variation among church forests across ecological and anthropogenic gradients allows for testing multiple hypotheses of the drivers of forest patch productivity (as measured by NDVI). Each point is a church forest in the study area, and many replicates exist for: (a)–(c) variables typically manipulated in fragmentation experiments including area, edge, and isolation effects; (d)–(f) environmental gradients including elevation, rainfall, and matrix characteristics; and (g)–(i) human factors including population, livestock density, and market access.

hypothesized based on a growing literature emphasizing links between diversity and ecosystem function; Cardinale et al. 2011, Gamfeldt et al. 2013) we performed another multiple linear regression showing the relationship between forest productivity and species richness for 27 church forests across four seasons. Applying the lm() procedure in R we regressed productivity on rarefied species richness as determined by field surveys. To account for abiotic and spatial variables that might have influenced both observed diversity and productivity, we also included area, elevation, and precipitation in the models (Loreau 2000, Haddad et al. 2017, Thompson et al. 2017). We again tested these regression results for potential spatial autocorrelation and corrected with SAR models as necessary (Dormann et al. 2007).

Finally to investigate whether human management in church forests might also influence forest diversity and productivity (Ostrom 2005, Aerts et al. 2016), we summarized findings from household surveys administered in six church villages – abbreviated here as Debresena, Woji, Ibanos, Alember, Robit Bata, and Gombat Michael. We explored how regional patterns in church forest species abundance distributions (SADs, Raunkiaer 1909) corresponded to church followers' preferences for planting and protecting seedlings of different species in their church forests. We also considered how these preferences might be influenced by perceptions of ecosystem services (including ecological, economic, and cultural benefits to church followers; Millennium Ecosystem Assessment 2005) from a subset of 12 native church forest tree species.

Results

Drivers of church forest productivity across environmental and anthropogenic gradients

In our sampled church forests, multiple linear regression results suggest variation in forest area, edge:area ratio, and vegetation density (NDVI) are related to both environmental and anthropogenic factors (Table 1). All environmental and anthropogenic variables considered in the initial (non-spatial) model are significant predictors of church forest vegetation productivity (Table 1c). Forests with larger areas and less fragmented forests (lower edge:area ratio) are associated with higher average NDVI values. Lower elevation and higher rainfall are associated with productivity, as is higher average NDVI in the surrounding matrix. Lastly, among the anthropogenic variables considered, higher livestock density is associated with decreased NDVI in the multiple linear regression model, while higher human population density exhibits a significant and positive association with average NDVI in the sampled church forests.

However, we also found evidence of significant spatial autocorrelation in the residuals of these initial models (Moran's I statistic p-value < 0.001), with the results of Lagrange Multiplier diagnostics suggesting that a spatial SAR error model is more appropriate for these data (Dormann et al. 2007). The coefficient estimates based on SAR error models were largely consistent with the initial multiple linear regression findings, though the effects of human population and livestock density were no longer significant predictors of forest productivity after accounting for spatial autocorrelation (Table 1).

Relationships between species diversity and church forest productivity

In keeping with a growing body of empirical work linking higher levels of multiple ecosystem services to the presence of more species diversity (Cardinale et al. 2012), we found that productivity in church forest patches was significantly and positively related to tree species richness (Fig. 5).

Even after controlling for fragment area, elevation, and precipitation – key spatial and abiotic factors that influence Afromontane plant communities (Wassie et al. 2010), there was a significant positive association between tree species richness and productivity in three of the four seasons considered (Table 2). The average annual NDVI (across all four seasons) was also significantly related to tree species richness. The observed relationship between productivity and diversity in church forests was most pronounced during the wet season (July, October) when overall productivity was highest, and less pronounced – or not significant – during the drier seasons.

We did not detect significant spatial autocorrelation in the residuals of four out of the five models (Table 2; Moran's I p-value > 0.298, specifying all sample church forests within 40 km as the neighborhood owing to the small sample and great distances between sample points). The model for mean NDVI in July exhibited some spatial autocorrelation, but the results of spatial SAR lag models (selected based on the Lagrange Multiplier test) yielded very similar coefficient estimates, with similar signs and magnitudes and even stronger statistical significance for the association between richness (20.857, $p < 0.001$) and richness^2 (–0.340, $p = 0.003$) and church forest productivity. (Supplementary material Appendix 3).

Integrating human management into interpretation of ecological patterns

Combining field data with survey data from priests and church member interviews offers the potential to identify (though not entirely tease apart) the possible roles of long-term human management which, combined with ecological

Table 1. Multiple linear regression models and SAR error models highlight systematic variation in area, edge:area, and average NDVI of church forests in south–central Amhara, Ethiopia. Models predict (a) church forest size, (b) edge:area ratio and (c) patch vegetation density (measured by NDVI). Covariates include forest fragment attributes, landscape context, and anthropogenic factors. Estimated coefficients are shown for multiple linear regression models (first column) and spatial SAR error models accounting for spatial autocorrelation (second column). Spatial autocorrelation was present in the residuals of all multiple linear regression models (Moran's I p-value < 0.001). Lagrange multiplier tests showed the spatial SAR error model to be more appropriate for the data than multiple linear regression or lagged alternatives (Dormann et al. 2007). Results of SAR error models accounting for spatial autocorrelation are qualitatively similar to non-spatial multiple linear regression model results for most variables, though the effects of anthropogenic influences are muted. *** < 0.001, ** < 0.01, * < 0.05.

	(a) Church forest area		(b) Edge:Area		(c) Average NDVI	
	Linear Regression Model	SAR Error Model	Linear Regression Model	SAR Error Model	Linear Regression Model	SAR Error Model
Patch attributes						
log(Area)			–0.438***	–0.432***	0.037***	0.023***
log(Edge/Area)					–0.029***	–0.042***
Landscape context						
log(Elevation)	–0.058	0.543	0.213***	0.004	–0.182***	–0.040*
Rainfall	0.008***	0.015***	–0.000	–0.000	0.002***	0.001**
Matrix NDVI 500 m	0.001***	0.001***	–0.000***	–0.000	0.001***	0.001***
Anthropogenic factors						
Population density	–0.065*	–0.073*	–0.006	–0.010	0.007**	0.001
Livestock density	0.000	0.002	–0.001**	–0.000	–0.000**	0.000
AIC	6201.5	5788.0	–1202.1	–1458.7	–7357.9	–8115.6
Moran's I	0.139***		0.084***		0.222***	

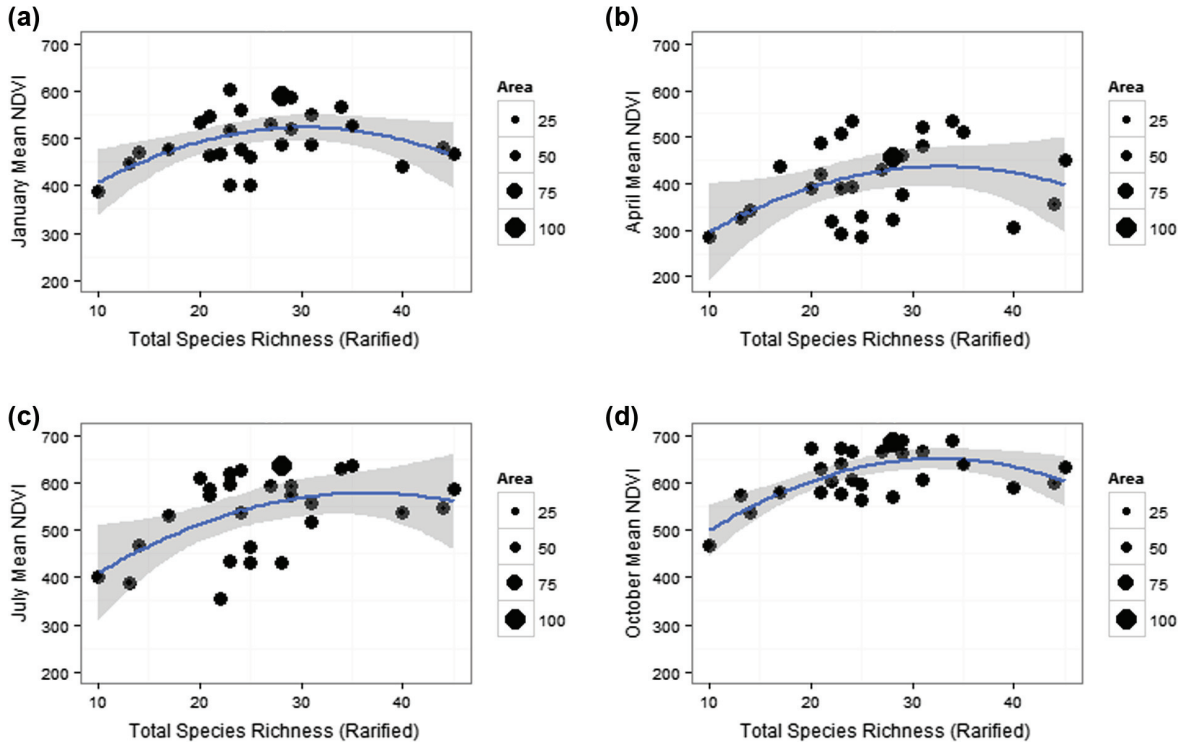


Figure 5. Productivity (NDVI) is positively associated with species richness in Ethiopian Orthodox church forests. Panels show average NDVI as measured using Landsat 8 satellite imagery for (a) January, (b) April, (c) July and (d) October for the years 2014–2015. There is a significant positive relationship between church forest productivity and rarefied species richness in January (short rainy season), July, and October (long rainy season). Point sizes reflect church forest area. Shaded areas represent 95% confidence intervals.

factors, may be generating observed patterns in species diversity and forest productivity. In general, native species followed the expected pattern: the most frequently occurring tree species were present at the highest densities (e.g. *J. procera*, *E. abyssinica*, *O. europaea*), and geographically restricted species were locally rare (e.g. *C. africana* and *F. vasta*, both restricted to low elevation church forests, Fig. 6a). By contrast, the native cash crop coffee (*C. arabica*) and the two non-native species (*E. camaldulensis*, *E. globulus*) grew at high densities but in a small proportion of forests (Fig. 6a).

Notably, the distribution and ranked abundance of native tree species (Fig. 6a) qualitatively mirrors the planting preferences expressed by local church members for planting (Fig. 6b). When asked in social surveys which five tree species should be prioritized for planting in their church forests, over two thirds of our 145 respondents across six church villages cited *J. procera*. Similarly *O. europaea* and *C. africana* were frequently cited as preferred species for planting, and both are present in relatively high numbers subject to ecological constraints (*O. europaea* restricted to higher elevation forests, and *C. africana* concentrated in lower elevations). In contrast, almost no respondents called for planting *E. abyssinica*, *M. lanceolata*, *H. abyssinica*, *A. digitata* or *F. vasta* (Fig. 6b). With the exception of *E. abyssinica*, which is present across multiple church forests in large numbers yet is not preferred for planting, these planting preferences largely mirror observed relative species abundances.

Our survey further asked about respondent perceptions of ecosystem services provided by the 12 native tree species in Fig. 6a–b across our six sample church forests. Services ranged from extractive uses (e.g. fuel and construction wood harvesting) to less extractive benefits such as food, medicine,

Table 2. Mean NDVI of church forests in south-central Amhara varies positively with species richness. Multiple linear regression models control for landscape context. NDVI ranges from 0–1, but NDVI units are scaled to 0–1000. For example, a 1-unit increase in tree species richness is, in January, associated with an 18.099 increase in scaled mean NDVI, corresponding to a 0.018-unit increase in estimated mean NDVI. Increased tree species richness is positively associated with church forest productivity in models (a) and (c)–(e). Moran's I statistic shows little evidence of spatial autocorrelation with the exception of model (c) for the month of July. *** <0.001, ** <0.01, * <0.05.

	(a) Mean NDVI January	(b) Mean NDVI April	(c) Mean NDVI July	(d) Mean NDVI October	(e) Mean NDVI Average
Richness	18.099**	15.369	19.209*	20.202***	18.220**
Richness^2	–0.323**	–0.266	–0.334*	–0.342***	–0.316**
Area	0.858	0.265	1.762*	0.815	0.925
Elevation	–0.0272	–0.095	–0.081	–0.034	–0.059
Rainfall	–0.587	0.926	–1.582	–0.828	–0.518
Multiple R^2	0.362	0.316	0.522	0.623	0.481
Moran's I	–0.045	0.015	0.107*	–0.139	0.015

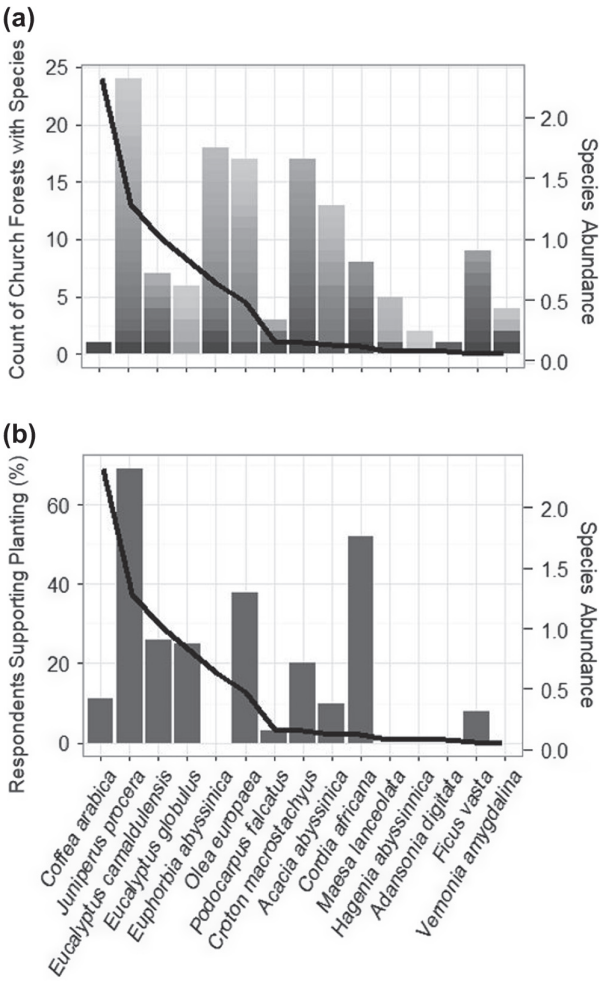


Figure 6. (a) Both occupancy and relative abundance of tree species vary among Ethiopian Orthodox church forests. Bars represent the number of church forests (n = 27) with a species present for 12 selected native forest species and three commercial species (*Coffea arabica*, *E. camaldulensis* and *E. globulus*) from among the 168 woody species identified (Wassie et al. 2010). Shading indicates individual church forests along an elevation gradient from low (dark) to high (light). The solid line shows the average count of each species per 10 × 10 m sampled plot across all sampled forests (secondary y axis). (b) Active management and planting may explain some variation in occupancy and abundance among church forests. Bars represent the percentage of church followers (n = 145 respondents) advocating planting seedlings for a given species in their church (n = 6 churches) for the 12 prominent indigenous forest species and three commercial species appearing in Fig. 5. The solid line again shows the average count of each species per sampled plot across our 27 sampled church forests (secondary y-axis).

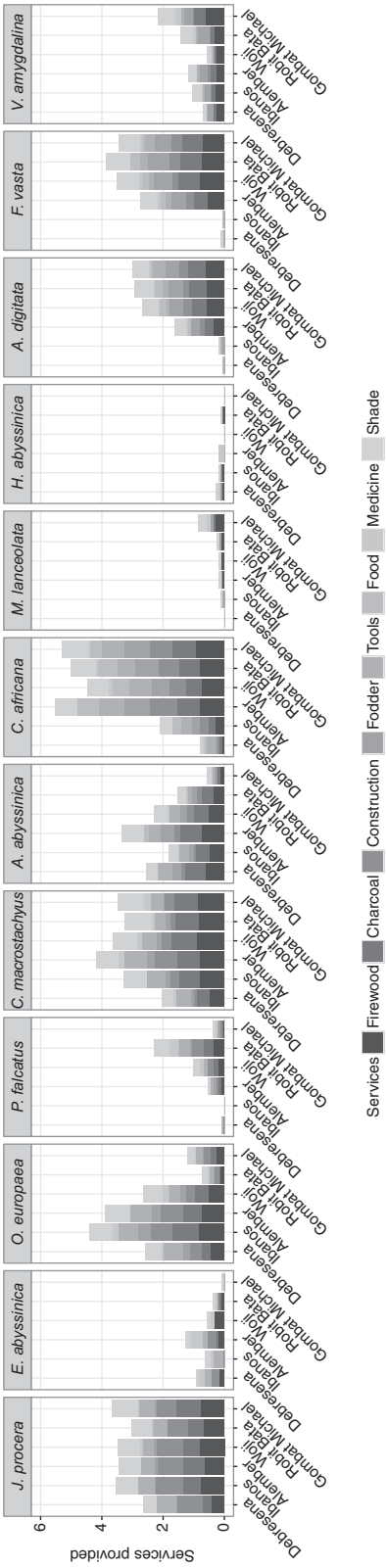


Figure 7. The perceived variety and extent of ecosystem services provided by 12 different tree species. Self-reported uses of 12 selected native tree species by local church followers, grouped by 1) high elevation (Debresena 3111 m and Ibanos 2447 m), 2) medium elevation (Alember 2290 m and Woji 2017 m), and 3) low elevation (Robit Bata 1934 m and Gombat Michael 1816 m). Shading indicates variety of services reported as being provided ("What benefits does this tree species provide?"), based on an 8-item checklist ranging from extractive benefits such as fuel or construction wood (darker shades) to non-extractive benefits such as food, medicine, or shade (lighter shades). Bar height indicates the proportion of survey respondents reporting each ecosystem service (maximum = 8 if all eight services were reported by 100% of respondents in that church community). Responses reflect a combination of species availability (i.e. presence or absence locally) and perceived benefits of that species.

or shade (Fig. 7). The number and type of ecosystem services reported by community members were largely congruent among species for pairs of forests at similar elevations, but varied across elevations (e.g. *A. digitata*, *F. vasta*, *E. abyssinica*, *P. falcatus*; Fig. 7). Patterns across forests show evidence of shared perceptions of species benefits for some widely distributed species – *J. procera*, *O. europaea*, *C. africana,* and *C. macrostachyus* – which were consistently reported across sites as offering the highest amount and diversity of ecosystem services. Both *J. procera* and *O. europaea* were especially valued (and both exhibit broad occupancy and also high

abundance). The two species that were perceived as offering the most services (*J. procera* and *C. africana*; Fig. 7) are also species that respondents to the survey reported as being priorities for planting (Fig 6b); however, they differ widely in their overall abundance (Fig. 6a).

Discussion

Comte et al. (2016) argue that ignoring the effects of anthropogenic influences may limit our ability to understand species' vulnerability and biodiversity changes under climate change in human-modified ecosystems (Gaston 2000, Brook et al. 2008). One way to better understand these multifaceted human drivers of forest degradation is to study them in contexts where ecological variation is great and anthropogenic variation relatively small. While differences in local management of the church forests that we studied exist, local knowledge – from priests and church followers – is also deeper and more accessible than in observational research in non-sacred sites (Mekonnen et al. 2016). By combining remotely sensed data with field data, our study illustrates how church forests and other sacred natural sites systems (Verchuuren et al. 2010) might help better understand relationships between forest productivity, species diversity, and human management in long-fragmented landscapes. Our results suggest that human influence, in part a function of longstanding Ethiopian Orthodox church rules surrounding species uses, combine with environmental factors to influence the distribution and abundance of tree species, as well as overall productivity of church forests. Consequently, our study highlights the potential for social and ecological data to jointly inform our understanding of fundamental ecological patterns.

At the landscape scale, productivity in church forest fragments appears to respond to variation in patch attributes (area, edge) and landscape characteristics (elevation, rainfall) in ways consistent with past experimental research and theory on fragmentation (Haddad et al. 2017). Our finding that livestock density was strongly negatively associated with forest size and productivity also corroborates previous work (Wassie et al. 2009) and further emphasizes threats posed by livestock to church forests. Other findings from our spatial analysis were unexpected – such as the apparent positive association between human population density and church forest productivity (measured by NDVI). Though we cannot definitively explain why greater human population is associated with more productive forest in our sample, we hypothesize that this reflects 1) increased protection of forests in population-dense areas with greater church membership and often more resources for guards and other rule enforcement (Ostrom 2005), and 2) greater access to non-forest sources of fuel and construction wood in population-dense areas, reducing demand for extractive forest resources. The observed positive effect of matrix productivity on church forest productivity may reflect both higher agricultural productivity (leading to greater matrix NDVI) as well as higher rates of *Eucalyptus* spp. planting near towns. *Eucalyptus* provides an alternative source of fuel and construction materials outside church forests (Liang et al. 2016), and may thus be linked with less wood collecting and higher productivity within forests. Combined these findings suggest that in sacred natural sites where local land-users have access to more non-livestock economic resources – either more productive agricultural land or alternative sources of fuelwood and timber – they may also be able to better maintain more productive native forest patches.

Our second set of findings – that there appears to be a significant relationship between woody species diversity and church forest productivity, even after controlling for elevation and precipitation, is also largely consistent with studies in smaller scale experiments (Cardinale et al. 2012). Though we controlled for some environmental factors, it is plausible that other abiotic factors such as soil nutrients (Aerts et al. 2006) or management strategies that vary across sites may be responsible for the patterns we observed (Fig. 5) – namely, the apparent decline in productivity at high diversity levels (Loreau 2000). Notably, we also found that diversity–productivity relationships vary across seasons. Our results suggest that if species and phenological diversity covary across sites, higher species diversity may allow fragments to more rapidly or more thoroughly capitalize on rainy season conditions favoring vegetation growth. More generally, our findings also suggest that future degradation or loss of more diverse church forest sites – or more diverse sacred natural sites elsewhere – will lead to substantial losses in productivity and associated ecosystem services (Chaplin-Kramer et al. 2015, Mokria et al. 2015).

Perhaps even more important, this initial investigation into diversity–productivity relationships also highlights the potential utility of church forests and other sacred natural sites not only for rigorous mensurative testing of fragmentation hypotheses, but also for studies of fundamental ecological patterns, beyond fragmentation per se. Our empirical examples in this paper represent improvements over simple observational studies with no controls, and because very few native forest patches exist in our study area outside of church forests (Ayalew et al. 2006, Tadele et al. 2014, Mekonnen et al. 2016), our study illustrates essentially the only realistic approach for addressing landscape-scale questions in the long-occupied, heavily degraded farmland covering much of northern Ethiopia. This is not to say that church forests do not also provide forest patches for some forms of experimental manipulation; for example, Wassie et al. (2009) constructed exclosures in two forests to investigate the influence of grazers on tree regeneration. Even more, observational data collected at a few forests (e.g. stream water quality (LoTemplio et al. 2016), soil quality (Liang et al. 2016), seed predation (Wassie et al. 2010)) could be expanded to include many forests that span landscape gradients and thereby test hypotheses at both local and landscape scales. This option is particularly enticing for questions at the ecosystem level where replication is challenging. Perhaps one of the most exciting avenues of potential experimental research that makes use of such 'replicate' sacred forests pertains to ecological restoration. Replicated landscape experiments in restoration are rare (Holl et al. 2003), but valuable for testing our understanding of large-scale ecological processes as well as directly increasing recovery of degraded landscapes surrounding sacred natural sites in Ethiopia and globally.

However, as emphasized in our final set of findings based on household surveys, viewing ecological patterns through the lens of past and ongoing human management informs (and perhaps even challenges) our interpretation of the mechanisms driving ecological patterns – both at the landscape and individual forest patch scale. Some anthropogenic influences on church forests are abundantly clear – for example coffee and *Eucalyptus* spp. have been intentionally planted in high densities, though at only a few forests. But in other instances human intervention may generate or reinforce patterns of distribution and abundance like those we might expect based on ecological theory. For instance, locally abundant species generally tend to also be widespread (Gaston et al. 2000). But in church forests it may be that some tree species are abundant both across and within forests because larger numbers are needed to provide desired ecosystem services, and thus communities actively plant and protect them (Fig. 6–7). For instance, while *J. procera* offers valuable properties as fuelwood and a source of sturdy, rot-resistant timber, it is also a religiously important tree traditionally used for church construction and repairs (Wassie 2002). This religious purpose likely explains the strong preference for planting *J. procera* across all surveyed church forest sites (including among respondents in sites where few or no *J. procera* is currently found). Even the case of *E. abyssinica*, which provides few reported ecosystem services (Fig. 7) and is not desired for planting (Fig. 6b) yet is present across many forests in high numbers (Fig. 6a) may also reflect perceived ecosystem services. The main benefits *E. abyssinica* offers are medicine and shade (both permitted uses in almost all church forests), creating a positive incentive for church followers to sustain existing trees and relatively few pressures to remove them.

A final exception to the expected abundance–distributional pattern was *F. vasta*, which occurs in many forests but is locally rare. One explanation may be its large size which could limit its density at the spatial scale of surveys in this study. However, it is useful to also consider that expressed interest in planting this species was relatively low (Fig. 6b). Moreover, the benefits to church followers are largely in the form of non-destructive uses such as fruit and shade in prayer spaces (Fig. 7), which ultimately may play a role in the persistence of this species in small forest patches. Overall, our data suggests that the ecological patterns we observe for presence, abundance, and community productivity in church forests may reflect both planting of desired species and also long-term management of existing species, perhaps because of the ecosystem services (ecological, economic, and cultural; Millennium Ecosystem Assessment 2005) the species provide.

Challenges and limitations to fragmentation research in sacred natural sites

Noteworthy challenges to sacred natural sites research include the availability and accessibility of suitable sites for mensurative experimental research, the generalizability of findings beyond local ecologies or beyond sacred natural sites systems, and concerns surrounding the cultural appropriateness of scientific research in sacred spaces. In trying to conduct a large-scale mensurative fragmentation experiment with very specific elevation, area, and other forest characteristic criteria to meet, it may become a challenge to assemble enough replicate forests based on costs, security concerns, or other factors influencing the accessibility of forests or the feasibility of monitoring over time. Even when suitable replicates can be found, concerns about external validity may remain: past research on sacred natural sites has largely concluded that while sacred sites can be effective modes of conservation, they do not translate easily to many national-level resource management categories, limiting their scope to pre-existing bio-cultural conservation systems (Maffi and Woodley 2012, Pungetti 2012, Gavin et al. 2015). Thus, while sacred natural sites provide a unique opportunity to control for relevant ecological and anthropogenic covariates and study fragments at a large spatial scale, extending results to other systems may be limited. Even within a given sacred site system there may be limitations to generalizability – in Ethiopia new church forests are being established rapidly near some growing towns and urban areas, for example, but many of these new church forest groves are comprised of *Eucalyptus* and other plantation species rather than native species (Wassie 2002, Wassie et al. 2005, Reynolds et al. 2015, Aerts et al. 2016, Liang et al. 2016), representing very different ecosystems from older church forests (and potentially limiting their value for many ecological studies).

A final important limitation to research in sacred natural sites is the significant institutional restrictions which may be imposed on researchers, ranging from complex or bureaucratic church and legal controls governing access to sites, to severe restrictions on allowable practices (e.g. disallowing species sampling, removal of samples, etc.). Although in some cases monetary compensation can offset perceived social taboo activities in forests, in other cases such exchanges may not be possible or may be inappropriate. Careful evaluation of community attitudes towards research activities, communication of research goals and findings, and concerted efforts to identify opportunities to involve and benefit local communities are important considerations to ensure the short- and long-term viability of research efforts (Lowman 2011, Berkes 2012, 2013). That said, in our research in church forest communities to date there has been strong community support for efforts to plant and protect native species in church forests – especially religiously significant and multi-use tree species such as *J. procera* or *O. europaea* – suggesting that at least in the northern Ethiopian context the institutional platform may exist for expanded research and restoration through partnerships with church communities.

Conclusions

Our study begins to respond to recent calls for expanded conservation research at the intersection of the ecological and social sciences (Stockwell et al. 2003, Berkes 2007, Bennett et al. 2009, Gagnon and Berteaux 2009, Pretty et al. 2009, Pereira et al. 2010, Kothari et al. 2012, Watts et al. 2016) for studying both the consequences of habitat loss and fragmentation, and strategies for restoring function to fragmented landscapes (Janzen 1988, Hooper et al. 2012, Lancaster et al. 2015). In church forest systems both species

diversity and forest patch productivity are clearly related to short- and long-term human influences. We highlight the potential for sacred natural sites systems to serve not only as key repositories of threatened biodiversity, but also as important reserves of knowledge about the past and present management and value of ecological systems (Ostrom 1990, 2010, Berkes 2012). Indeed, sacred natural sites systems provide the potential to inform pressing debates surrounding management of fragments in production and multi-use landscapes (Haddad et al. 2014), and also for broadening our understanding of the ecological and anthropogenic processes characteristic of forest fragments in rural communities in the developing world.

By providing opportunities to control statistically or experimentally for both ecological and anthropogenic sources of variation, church forests and other sacred natural sites allow for a more comprehensive and systematic consideration of the degree to which traditional ecological knowledge and other social science data can inform our understanding of ecological patterns in multi-functional landscapes.

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Supplementary material (Appendix ECOG-02950 at <www.ecography.org/appendix/ecog-02950>). Appendix 1–3.

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