Deforestation in an African biodiversity hotspot: Extent, variation and the effectiveness of protected areas

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Jonathan M.H. Green [a,b,*], Cecilia Larrosa [c,d], Neil D. Burgess [d,e,f], Andrew Balmford [b], Alison Johnston [g], Boniface P. Mbilinyi [h], Philip J. Platts [i], Lauren Coad [d,j,k]

[a] Woodrow Wilson School of Public and International Affairs, Princeton University, Princeton, NJ 08544, USA
[b] Conservation Science Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK
[c] Department of Life Sciences, Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot SL5 7PY, UK
[d] United Nations Environment Programme World Conservation Monitoring Centre, 219 Huntingdon Road, Cambridge CB3 0DL, UK
[e] Center for Macroecology, Evolution and Climate, Department of Biology, University of Copenhagen, Denmark
[f] Conservation Science Program, WWF-US, 1250 24th Street, Washington, DC, USA
[g] British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, UK
[h] Department of Agricultural Engineering and Land Planning, Sokoine University of Agriculture, P.O. Box 3003, Morogoro, Tanzania
[i] The York Institute for Tropical Ecosystems (KITE), Environment Department, University of York, Heslington, York YO10 5DD, UK
[j] School of Geography, Environmental Change Institute, University of Oxford, Oxford OX1 3QY, UK
[k] School of Geography, Planning and the Environment, University of Queensland, Brisbane, QLD 4072, Australia

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ABSTRACT

The Eastern Arc Mountains of Tanzania show exceptional endemism that is threatened by high anthropogenic pressure leading to the loss of natural habitat. Using a novel habitat conversion model, we present a spatially explicit analysis of the predictors of forest and woodland conversion in the Eastern Arc over 25 years. Our results show that 5% (210 km^2) of evergreen forest and 43% (2060 km^2) of miombo woodland was lost in the Eastern Arc Mountains between 1975 and 2000. Important predictors of habitat conversion included distance to natural habitat edge, topography and measures of remoteness. The main conservation strategy in these mountains for the past 100 years has been to develop a network of protected areas. These appear to have reduced rates of habitat loss and most remaining evergreen forest is now within protected areas. However, the majority of miombo woodland, an important source of ecosystem services, lies outside formal protected areas, where additional conservation strategies may be needed.

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1. Introduction

Forest area in Africa decreased by an estimated 34–41 thousand km^2 per year during the 1990s and 2000s (FAO, 2010). Tropical moist forests are amongst the most species-rich terrestrial habitats on Earth, making deforestation a crucial issue for biodiversity conservation (Joppa and Pfaff, 2011; Pimm et al., 2001). Furthermore, they sequester and store large amounts of carbon; tropical deforestation is estimated to contribute 7–14% of global carbon dioxide emissions, resulting in accelerated climate change (Harris et al., 2012; IPCC, 2007). Given forests' crucial role in conserving biodiversity and mitigating climate change, as well as in sustaining local livelihoods, understanding the drivers and threat mechanisms of

forest conversion and finding ways to reduce rates of loss is high on the conservation agenda (Balmford et al., 2009).

An increasing research focus on the rates and predictors of habitat conversion has been aided by the advent of satellite remote sensing technologies (DeFries and Townshend, 1999). Regression models have been widely used to identify predictors of habitat conversion and previous studies have investigated the impact of market access (e.g. distance to roads and population centres) and topography (e.g. slope and elevation) at study scales ranging from sub-national (Patarasuk and Fik, 2013; Serneels and Lambin, 2001; Vuohelainen et al., 2012) to regional (Pfeifer et al., 2012; Portillo-Quintero et al., 2012) and global (Scrieciu, 2007). These models have been used to elucidate threat mechanisms of habitat conversion and to investigate the effectiveness of conservation efforts to prevent it. Predictive models have more recently been proposed as a tool for protected area planning: by assessing threats spatially and designating protected areas accordingly the potential impact of reserves can be maximised (Joppa and Pfaff, 2009). Predictive

models can also help in conservation resource allocation by suggesting different levels of investment required in different parts of a protected area network (Andam et al., 2008). Lastly, an international scheme to decrease the amount of carbon released into the atmosphere (Reduced Emissions from Deforestation and Degradation; REDD) requires an assessment of baseline (current) levels of habitat conversion and the future trajectories of loss to be estimated (Brown et al., 2007).

Much of our current knowledge of the causes and mechanisms of habitat loss is based upon research undertaken in Latin America and Asia, where deforestation is driven by agricultural exports and urban population growth, largely mediated through agricultural expansion, infrastructure development and resource extraction (DeFries et al., 2010; Geist and Lambin, 2002). However, the drivers and extent of deforestation have been found to vary between continents and Africa, in particular, has had few studies devoted to spatial modelling of habitat loss (Achard et al., 2002; DeFries et al., 2010; Fisher, 2010; Geist and Lambin, 2002; Pfeifer et al., 2012). We focus on the Eastern Arc Mountains in Tanzania where, although anthropogenic pressures are high, they vary across the landscape (Brooks et al., 2002; Burgess et al., 2006). Our objectives are to develop the first spatially explicit, high-resolution model of past evergreen forest and miombo woodland change in the Eastern Arc Mountains, based upon potential predictors of habitat loss and retention. We then use this model to predict likely future changes and to consider how habitat loss varies between protected and non-protected areas.

2. Study area

The Eastern Arc Mountains are a chain of ancient crystalline mountain blocs in East Africa under the climatic influence of the Indian Ocean (Lovett, 1985; Platts et al., 2011). In Tanzania, the range consists of 12 blocs running from the southern highlands to the northeast border with Kenya and covering over 50,000 km². The forests of the Eastern Arc are important centres of biodiversity and the mountains host 400–500 strictly-endemic vascular plant species, around 20% of which are trees (Platts et al., 2010, 2011), and at least 96 endemic vertebrate species (Burgess et al., 2007a). The Eastern Arc Mountains also support millions of people as they are a major source of water for drinking, agriculture, hydropower and industrial use while their forests and woodlands provide fuelwood, construction poles, charcoal and medicines (Burgess et al., 2007a; Swetnam et al., 2011).

However, the Eastern Arc Mountains have also experienced historically high rates of habitat loss that, in concert with their exceptional biodiversity, have led to their recognition as part of a globally-important biodiversity hotspot (Burgess et al., 2007a; Mittermeier et al., 2004; Myers et al., 2000). It is estimated that the Eastern Arc Mountains have lost 80% of their total preclearance forest extent, with 75% occurring before 1955 (Hall et al., 2009). The main reported threat mechanisms are conversion to agriculture, logging for timber, fire, and the collection of woody biomass for firewood and production of charcoal (Burgess et al., 2007a; Schaafsma et al., 2012). The slowdown in deforestation since 1955 is thought to be due to the fact that much of the remaining forest is in rugged terrain at high altitudes, and because most remaining forest lies within some form of protected area (Hall et al., 2009). Approximately 20% of the total area of the Eastern Arc Mountains falls within protected areas, which set restrictions on permitted extractive activities (Green et al., 2012; IUCN and UNEP-WCMC, 2010). Most of the protected areas are national forest reserves that were established prior to the 1970s for logging (banned in 1985), the conservation of water flow regimes, and the prevention of erosion (Haule et al., 2002; Neumann, 2002).

3. Materials and methods

3.1. Quantifying habitat loss

Woody vegetation in the Eastern Arc falls into two very distinct habitats. The first is closed canopy evergreen and semi-evergreen vegetation growing up to 40 m tall and with exceptional biodiversity value. The other is closed to nearly-closed canopy deciduous vegetation, known as miombo woodland, growing up to about 30 m tall and with lower biodiversity values (Burgess et al., 2004). Throughout this paper, we refer to these two habitat types as "forest" and "woodland", respectively. The distinction between these habitat types is common in East Africa and is important. As well as differing in their biodiversity, forest and woodland also differ in the types and amounts of ecosystem goods, such as timber, charcoal and medicinal plants, that they provide and their likely exposure to threats (Burgess et al., 2010; Swetnam et al., 2011); we therefore modelled forest and woodland loss separately.

We investigated habitat loss over the 25-year period prior to the year 2000. Given the relatively small amounts of forest converted over recent years, it is advantageous to consider a relatively long time period. This gives a greater number of conversion events upon which statistical models of habitat loss can be built and thereby improves projection accuracy (Sloan and Pelletier, 2012). Although it is possible that drivers of habitat loss have changed since the mid-1970s, several studies suggest that this is not the case for East Africa (DeFries et al., 2010; Fisher, 2010; Rudel et al., 2009). To assess land cover change we used published data from the Forestry and Beekeeping Division of Tanzania's Ministry of Natural Resources and Tourism (Table 1; Hall et al., 2009; Mbilinyi et al., 2006). These data map the changes in the extent of forest and woodland at 30 m resolution between two points in time, 1975 and 2000 (or as close to these years as possible, subject to the availability of cloud-free images; 1975 data were resampled to 30 m to allow pixel by pixel comparison to 2000).

Land cover change was assessed using Landsat MSS and Landsat ETM+. Images were obtained from the long dry season (July–November) or from the middle of the short dry season (January–February) to minimise cloud cover and seasonal differences. Images were rectified and enhanced (bands 4, 5, 3; contrast stretched using a Gaussian distribution function) using ERDAS IMAGINE software (ERDAS, 1999). Land cover classification, based on the methods described in Harper et al. (2007), was done using a supervised maximum likelihood classifier. Training was semi-automated and iterative: signatures of each land cover were created based upon a minimum of 30 pixels per land cover class, generated by on-screen digitising of selected areas for each land cover class derived from composite. Photo elements such as texture, colour, and local knowledge were used to guide land cover identification. The Signature Alarm command (ERDAS, 1999) was used to classify every pixel in the landscape according to the decision rule. The output was checked against both images in the satellite image pair. Errors were corrected through the creation of additional signatures and by editing the training sites of existing signatures (Hall et al., 2009; Harper et al., 2007; Mbilinyi et al., 2006). Only once visual inspection of the classification showed no further obvious errors did this iterative process stop. Maps were then verified by key informants from the Tanzania Forest Conservation Group, United Nations Development Programme-Global Environment Facility, World Wildlife Fund, Wildlife Conservation Society, CARE, Frontier-Tanzania, University of Copenhagen, and Museum of Trento, Italy. Multiple classified scenes were then mosaicked using ERDAS IMAGINE software to produce one change map for the Eastern Arc Mountains. Full details of image selection, processing, classification and verification are given in Mbilinyi et al. (2006).

Table 1
Description and sources for spatial data their derived products. Unless stated, reference year is 2000. Land cover change is described between 1975 and 2000, so variables used as predictors in our models of habitat loss that are expected to have changed over this period were also estimated for 1975 where possible (asterisk). Reasons for exclusion of predictor variables from the full model are also given.

Variable	Description	Exclusion from full model
Land use change (1975–2000)	We used a Landsat (MSS and ETM+) derived product that maps changes in forest and woodland extent between 1975 and 2000 for 30 m by 30 m pixels (Mbilinyi et al., 2006). These data are detailed in Section 3.1. These were resampled (nearest neighbour) to 25 m resolution and then aggregated to 500 m pixels of habitat loss (>50 % of 25 m pixels deforested) or retention (<50 % of 25 m pixels deforested). This made analyses more computationally tractable and gave greater consistency between the resolution of the response variable and predictor datasets	–
Distance to edge (m)*	Forest and woodland was mapped based on land use change map at 30 m resolution (see previous). The land cover types (woodland and forest) are combined for this measure so that the nearest edge to a patch of forest could be the far side of a piece of adjoining woodland (and vice versa). Euclidean distance to habitat edge was then calculated at 500 m resolution both for 1975 and for 2000, so that core forest or woodland areas received highest values, whilst areas that were not forest or woodland were set at zero. This measure was used because it is expected that natural resource extraction will be higher at the edges of natural habitat	–
Travel time (min)	Estimated travel time (min) to nearest city with a population greater than 50,000 in the year 2000 (Nelson, 2008). This derived product is provided at 30 arcsecond resolution and is based upon populations centres, transport networks, political boundaries, land cover and topography and full details can be found at http://bioval.jrc.ec.europa.eu/products/gam/sources.htm. Layer was resampled (bilinear interpolation) to 500 m	–
Distance to roads (m)	Main roads in the year 2000 (paved or are high quality gravel) were mapped by the Valuing the Arc project (see Swetnam et al., 2011 for details). Euclidean distance to main roads was then mapped at 500 m resolution	–
Distance to markets (m)	Village and town population data were compiled as part of the Valuing the Arc project (Burgess et al., 2009; http://www.valuingthearc.org/). Settlements with over 5,000 people were classed as markets and Euclidean distance to these towns was mapped at 500 m resolution	In forest analyses, it correlated with population pressure (>0.7), which was a better predictor of forest loss. It was included in woodland models.
Altitude (m.a.s.l.)	Digital elevation data were from the Shuttle Radar Topographic Mission, processed to fill data voids (Jarvis et al., 2008). Data are provided at 90 m resolution and can be accessed at http://srtm.csi.cgiar.org/. Layer was resampled (bilinear interpolation) to 500 m	–
Slope (°)	Slope was calculated using the *Slope* tool in the Spatial Analyst toolbox of ArcGIS using the altitudinal data (Jarvis et al., 2008; see previous), at 90 m resolution, as input. Layer was resampled (bilinear interpolation) to 500 m	–
Land value (USD ha^{-1} y^{-1})	Potential land value was estimated using data on maize and bean yields from Thornton et al. (2009), combined with survey data on crop values and input costs. Full details of the input data and methods for creating this layer are given in the S1 and in Green (2012). Layer was provided at 10 arcminutes and resampled (bilinear interpolation) to 500 m	–
Distance to water (m)	Rivers were mapped using the digital elevation model (see altitude layer below), using the methods described in S1. Euclidean distance to rivers was then mapped at 500 m resolution	–
Annual precipitation (mm)	Annual precipitation data are from the Tropical Rainfall Measuring Mission (1997–2006), processed by Mulligan (2006) to derive 1 km monthly grids of surface-received orographic rain. Mean monthly values were summed to give average yearly totals and resampled (bilinear interpolation) to 500 m	Excluded because it correlated with Water deficit, which was a better predictor
Water deficit (days)	Water deficit is a proxy for dry season length and severity. It is calculated as the highest cumulative deficit in mean monthly rainfall (derived data from Mulligan, 2006), where deficit <30 mm per month (Platts et al., 2010). Data are at 1 km resolution, and resampled (bilinear interpolation) to 500 m	–
Population density* (people km^{-2})	Human population data were estimated using the derived product LandScan 2008 (Bright et al., 2009). This layer is a modelled surface, based upon administrative boundaries, land cover data, topography, roads and population centres. It has been further modified to exclude populations from National Parks and Game Reserves and to match ward-level census data for the year 2002 (NBS, 2002; Platts et al., 2011). Population density was also estimated for 1975 using ward-level population growth rate data (NBS, 2002). LandScan 2008 is provided at 1 km resolution and resampled (bilinear interpolation) to 500 m	Highly correlated with population pressure (>0.7), but a poorer predictor. Therefore, population pressure layers were used instead
Population pressure* (people equivalents)	Population pressure was calculated from population density data according to the methods described in Platts (2012) and in S1. This variable was also calculated based upon the population density data that were hindcast to 1975 based on ward-level population growth rates (see previous). Layer was resampled (bilinear interpolation) to 500 m	–
Protected areas	Shapefiles were from the World Database on Protected Areas (WDPA; IUCN and UNEP-WCMC, 2010), modified to include recently designated protected areas (MNRT, 2010) and correct spatial errors (see Larrosa, 2011 for detailed description). Data included information on 142 protected areas and were rasterised at 500 m resolution (maximum combined area in *Polygon to Raster* tool in ArcGIS)	N/A: protected area status was not a potential predictor. It was used to identify non-protected sites, upon which the models were based
Bloc	The mountain blocs were defined using shapefiles provided by Platts et al. (2011). Data were rasterised at 500 m resolution (maximum combined area in *Polygon to Raster* tool in ArcGIS)	–

All variables were projected using WGS 1984, Zone 37S.

Pixels were aggregated to 500 m resolution by summing the area of forest retained, forest degraded, woodland retained and woodland degraded within each 500 m analysis unit (ArcGIS Spatial Analyst toolbox). Using 500 m resolution allowed for analysis at the fine-scales needed by conservationists in the region (median protected area size is 8.8 km^2; Green et al., 2012) and is consistent with the resolution of other spatially explicit data used in these analyses (Table 1). This resolution is also computationally tractable for the construction of non-parametric models over a large area.

We calculated rates of habitat loss as the total decrease in habitat (woodland or forest) between 1975 and 2000, divided by the area of habitat in 1975. We converted compound losses over 25 years into annual rates of loss using the equation $r = 1 - (1 - A)^{(1/t)}$, where r is the proportion lost per annum and A is the total proportion lost over the 25 year time period, t.

3.2. Potential predictors of change

We obtained spatially explicit data for 12 potential predictor variables chosen for an a priori expectation of their effect on the response variable (Lukacs et al., 2010; see Table 1 for data sources and definitions): distance to natural habitat edge, travel time to large cities, distance to main roads, distance to markets, and topography (which was included as a smoothed interaction between altitude and slope) were all chosen because they are related to the amount of time that is required to access the land and to transport goods to markets. Land value, distance to water, annual precipitation, and water deficit are all related to the potential productivity of the land under agriculture.

In addition to these variables we used two population-based measures of local demand for agricultural land or natural resources. Population density data came from LandScan 2008 (Bright et al., 2009), which were corrected to match the absolute numbers reported in Tanzania's 2002 National census (NBS, 2002) according to methods in Platts et al. (2011). We also used these population density data to derive estimates of population pressure, a measure which recognises that anthropogenic pressure accrues not just from the population at a given location but also from nearby populations (Ban et al., 2009; Green et al., 2012; Platts, 2012). The method is described in detail in Appendix S1.

Where data for potential predictors were available for 1975 (see Table 1), we used these to build models of habitat loss over the following 25 years, otherwise data were from 2000. All geographic information was processed in ArcGIS 10 (ESRI, 2010).

3.3. Model construction

We used generalised additive logistic models to predict habitat loss (binomial response) between 1975 and 2000, where loss was defined as areal reduction of at least 50% in a given 500 m pixel. Generalised additive models are based on general linear models, but they are able to incorporate non-parametric relationships between the explanatory and response variables, so are not constrained by assuming a particular functional form (Brown et al., 2002; Hastie and Tibshirani, 1990; Mendes and Junior, 2011; Rutherford et al., 2008; Wood, 2006). We only used cells with ⩾50% forest or woodland at the start of the period. Importantly, we built our models using only forest and woodland outside of protected areas as such land tenure systems might be expected to reverse trends found in unprotected areas. Protected area data are from World Database on Protected Areas (IUCN and UNEP-WCMC, 2010), modified to include recently designated protected areas and to correct spatial errors (Table 1; MNRT, 2010; see Larrosa, 2011 for details).

When potential predictor variables were intercorrelated by 0.7 or more (Spearman rank correlation coefficient) just one was used in the full model (Table 1). Initially, we constructed a full model containing all remaining potential predictors (Lukacs et al., 2010). To arrive at a minimal adequate model, we assessed terms by looking at their estimated degrees of freedom, whether the confidence region includes zero throughout the scale of the potential predictor and whether their deletion led to an increase in Akaike's Information Criterion (AIC) or General Cross Validation (GCV) score (Wood and Augustin, 2002). In order to avoid over fitting, we took three precautions. First, in estimating the generalised cross validation score, we increased the penalty term (gamma) for using an extra degree of freedom from 1 to 1.4 (Wood, 2006). Second, we set the maximum number of allowed basis dimensions for smoothed terms (not including tensor products) to four (Platts et al., 2008). Third, smooth relationships were visually examined to check for overfitting. Where smooth terms were not realistic, the degrees of freedom were reduced.

To account for the effect of spatial autocorrelation in our models, we included in all models mountain bloc as a random effect (see Table 1; Platts et al., 2011) and the interaction of latitude and longitude as a smoothed term. We also tested models to check for any unexplained spatial clustering at local scales: spatial autocovariate terms were constructed by calculating, for each pixel, a distance-weighted mean across model predictions in neighbouring cells (Platts et al., 2008). Seven autocovariate terms were calculated for each model using increasing neighbourhood sizes (range: 1.5–10.5 km^2). We then added each of these in turn to our model to test which gave the greatest increase in explained deviance.

We conducted all statistical analyses in R 2.13.1 (R Development Core Team, 2009) using the package 'mgcv' to construct generalised additive models (Wood, 2011).

3.4. Goodness of fit

We assessed goodness of fit using receiver operating characteristic curves. Calculating the area under the curve (AUC) gives an estimate of the fit of the model to the data, with values varying between 1, a perfect model, and 0.5, a model that is no better than random. We used the 'pROC' package in R to plot the fraction of true positives against the fraction of false positives for a series of possible thresholds (Robin et al., 2011). The AUC estimate was cross-validated by partitioning the dataset into five equal-sized, stratified groups, such that each contained similar proportions of habitat loss and retention (Platts et al., 2008). The model was parameterised using four of the five partitions, leaving out one partition as pseudo-independent test-data. Repeating this procedure five times, each time retaining a different test set, produced the final cross-validation index.

3.5. Protected area effectiveness

Although we can compare rates inside and outside of protected areas, this does not account for spatial variation in value and corresponding likelihood of conversion. In particular, protected areas may be biased towards being located in areas that are unlikely to be converted even in the absence of such protection (Joppa and Pfaff, 2009). In order to control for this, we fitted the models using pixels that were not protected in 2000 (see Section 3.3), and then extrapolated to protected area pixels. Comparing these estimated rates (in the absence of protection) to the observed levels of conversion then provided a measure of protected area effectiveness, which controls for variation in exposure to threat (Vuohelainen et al., 2012). Thus, if r_e is the expected rate of loss and r_o is the

observed rate, we calculated effectiveness (E) as the percentage decrease in habitat loss: $E = (r_e - r_o)/r_e * 100$.

3.6. Predicting future habitat conversion rates and mapping areas under threat

For all cells with at least 50% forest or woodland cover in the year 2000, we predicted annual rates of habitat loss by incorporating up-to-date information on predictors. We then considered how the threat of habitat conversion has changed between 1975 and 2000 by comparing modelled average annual rates of habitat loss for 1975–2000 with those predicted for the period 2000–2025.

4. Results

4.1. How much habitat conversion has occurred in the EAM in the last 25 years?

We estimate that 26% (2274 km^2) of forest and woodland was lost between 1975 and 2000 in the Eastern Arc, with the rate of habitat conversion lower in forest (5%/25 y) than in woodland (43%/25 y; Fig. 1a and b; Table 2). There was marked contrast between rates of loss in protected and unprotected areas: forest in protected areas was lost at approximately one third of the rate found outside protected areas (4% and 11% respectively), while woodland in protected areas was lost at approximately two thirds of the rate found in unprotected areas (33% and 45% respectively; Fig. 1 and Table 2). Of the remaining forest area, 74% is within protected areas, compared to 32% for woodland.

4.2. What predicts spatial variation in conversion rates?

Our models showed high cross-validated goodness of fit with an AUC of 0.85 (forest) and 0.84 (woodland). Although the smoothed interaction of longitude and latitude was an important predictor (reduction in deviance explained was 5% and 7% for forest and woodland respectively), its removal did not alter the direction of the relationships observed, which is evidence that its inclusion is

not masking or altering the effect of important environmental or socio-economic gradients. When we tested for residual spatial autocorrelation at local scales, we found minimal effect: For forest loss, the highest increase in explained deviance was obtained from an autocovariate term based on a neighbourhood size of 1.5 km^2, which increased the percentage of explained deviance from 30.4% to just 31.1%. For woodland, the greatest increase was when an autocovariate term based on 17 km^2 was used but the increase in explained deviance was minimal (from 28.3% to 28.9%).

4.2.1. Forest model

The latitude:longitude interaction was the most important predictor of forest loss, which suggests that spatial autocorrelation is high (Table 3). Topography was the next most important predictor. The relationship shows that habitat conversion peaked around 1000–1200 m.a.s.l., particularly in flatter terrain. In the steepest terrain habitat conversion appeared consistently low across the altitudinal range (Fig. 2a). Distance to the habitat edge ('habitat' includes both forest and woodland) was also an important predictor, with the likelihood of habitat conversion decreasing rapidly as distance to edge increases. However, at distances of more than 1.5 km, the relationship levelled out (Fig. 2a). In addition, the probability of habitat conversion declines rapidly when travel time to large cities exceeds 12 h. The relationship with distance to main roads showed an initial decrease in probability of conversion with distance, followed by an increase. Increased distance to water was associated with lower habitat conversion probabilities; however, there was a humped relationship between land value and habitat conversion, showing an initial increase in habitat conversion with land value, followed by a decrease (Fig. 2a).

4.2.2. Woodland model

Topography and distance to habitat edge were the most important predictors of woodland loss after latitude:longitude and mountain bloc (Table 3). Woodland loss decreased with increasing altitude, except for a marked hump at mid-elevations (around 1100 m.a.s.l.) in less rugged terrain, while woodland loss showed an almost linear relationship with distance to edge (Fig. 2b). In-
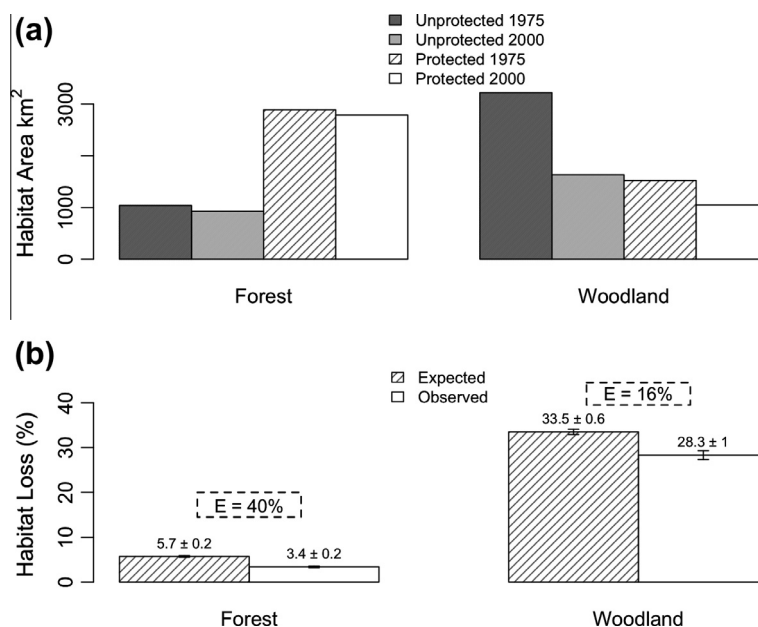

Fig. 1. Forest and woodland loss in the Eastern Arc Mountains. (a) The area of forest (left hand group) and woodland (right hand group) is shown for 1975 and 2000. (b) For protected areas, the mean (±2 standard errors) expected (hatched bars) and observed (white bars) rates of forest and woodland loss per pixel between 1975 and 2000 are shown as a percentage of the area in 1975. Effectiveness scores (E) are shown within dashed boxes.

Table 2
Deforestation in the Eastern Arc Mountains by protection status (in year 2000) for forest and woodland. In total, 26.2% of forest and woodland was lost between 1975 and 2000; however, this varied considerably by habitat type and protected area status. For both woodland and forest cells, mean modelled losses for the period 1975–2000 (assuming no effect of protection) are shown in grey. These are slightly higher than mean observed loss per cell for protected areas and slightly lower than mean observed loss per cell for unprotected areas (upon which models are based).

	Protected areas	Unprotected	Total
Forest			
Area 1975 (km^2)	2889	1040	3928
Area 2000 (km^2)	2787	928	3715
Average loss (% y^{-1})	0.1	0.5	0.2
Observed 25-year loss (%)	3.4	10.1	5.1
Modelled 25-year loss (%)	5.7	7.4	6.1
Woodland			
Area 1975 (km^2)	1521	3222	4743
Area 2000 (km^2)	1049	1633	2682
Average loss (% /y)	1.5	2.7	2.3
Observed 25-year loss (%)	28.3	46.2	39.8
Modelled 25-year loss (%)	33.5	44.7	40.7

creased remoteness, in the form of distance to markets and main roads showed a generally negative correlation with conversion likelihood. Lower water deficit – a proxy for higher productivity – appeared to be associated with greater probability of conversion; however the association with land value was less clear (Fig. 2b) – an initial sharp increase was followed by a decrease, which then tailed off.

4.3. Conservation effectiveness

Observed levels of habitat loss were considerably lower inside protected areas than in non-protected cells (Fig. 1a). After accounting for underlying spatial variation in conversion probability using modelled estimates, observed rates were still 40% lower than expected for forest and 16% lower for woodlands (Fig. 1b).

4.4. Where is pressure likely to be highest from 2000 to 2025?

If forests and woodlands continue to be lost at the same rates that we observed between 1975 and 2000, then our models predict that by 2025 we can expect to have lost a further 5% (197 km^2) of forest and 42% (1130 km^2) of woodland. However, these absolute rates are likely to change; extraction of natural resources will be-

come more difficult as remaining forest and woodland will be the least accessible (perhaps limiting supply) whilst population growth is likely to increase demand. When mapped across the Eastern Arc Mountains, annual probabilities of conversion for 2000 showed substantial spatial heterogeneity (Fig. 3; S2). In particular, areas on the edge of mountain blocs (closer to markets and generally with higher population pressure) were likely to come under higher conversion pressure. The East Usambara Mountains experienced the highest levels of habitat loss over our 25-year study period and also have amongst the highest levels of threat predicted for 2000–2025 (S2). For forests, the West Usambaras, Ukugurus and Rubehos show the highest levels of future pressure, whilst for woodlands, the South Pares, Ukagurus and Rubehos show highest future threat (Fig. 3b; S2). In addition, woodlands of the southeastern flanks of the Udzungwas are also expected to face high pressure to 2025 (Fig. 2b).

5. Discussion

Conservationists are justifiably concerned about forest loss in the Eastern Arc Mountains due to their exceptionally high levels of biodiversity (Burgess et al., 2007a; Hall et al., 2009). However, our results point to another important habitat within the Eastern Arc Mountains. Although less biodiverse (Burgess et al., 2004), woodlands are undergoing far greater rates of conversion than forests, both inside and outside of protected areas (see also Mbilinyi et al., 2006). This should be of interest from both conservation and development perspectives. Woodlands provide ecosystem services whose utilisation at unsustainable rates is likely to be a cause of the observed losses (e.g. charcoal use in Ahrends et al., 2010). The current use of woodlands by local communities for ecosystem goods, particularly charcoal and firewood (Schaafsma et al., 2012), may also have the effect of buffering adjacent forests from higher rates of extractive use. For example, pressure in woodlands along the southeastern Udzungwas is many times greater than that in the forests that lie adjacent to them farther into the mountains. The woodlands also contribute to the conservation of ecological processes, such as the annual migrations of elephant and buffalo between protected areas (Jones et al., 2009). It is of concern, therefore, that just 32% of remaining woodland extent (22% of 1975 extent) falls within protected areas.

The forests of sub-Saharan Africa are expected to retain historical patterns of conversion with forest loss largely driven by small-

Table 3
Predictor variable contribution to models. Variables that were dropped from the minimal adequate model are indicated with square brackets. The contribution of predictor variables was assessed through calculating the percentage decrease in deviance explained and the absolute change in AIC and GCV scores when the term was dropped from the minimal model (if the term was kept in the minimal model) or from the full model (if the term was dropped to reach the minimal model). The total percentage deviance explained in the minimal adequate model was 30.4% (forest model; $n = 3919$) and 28.3% (woodland model; $n = 10,362$).

Predictor	Forest model					Woodland model				
	EDF	ΔGCV	ΔD$_2$	ΔAIC	AIC rank	EDF	ΔGCV	ΔD$_2$	ΔAIC	AIC rank
Distance to habitat edge	1.9	−347.6	−2.6	51.1	3	2.3	276.4	−1.6	221.7	3
Travel time	2.6	−5.4	−1.6	28.8	6	[1.7]	[−49.1]	[−0.1]	[7.3]	[11]
Distance to road	2.1	−97.9	−0.5	6.1	8	2.9	−74.7	−0.5	63.3	6
Distance to market*	–	–	–	–	–	2.0	−120.6	−1.1	149.1	5
Population pressure ($\sigma = 25$)	[0.5]	[−18.4]	[0.0]	[−0.4]	[9]	–	–	–	–	–
Population pressure ($\sigma = 50$)	–	–	–	–	–	[1.3]	[−133.1]	[0.1]	[−12.9]	[10]
Land value	2.5	−281.4	−1.8	31.5	5	3.9	87.0	−0.4	51.9	7
Distance to water	1.8	5.5	−0.5	15.1	7	[0.3]	[−104.1]	[0.1]	[−15.6]	[9]
Water deficit	[1.1]	[56.8]	−0.1	[−0.1]	[8]	1.6	−114.1	−0.2	30.7	8
Altitude:Slope	6.5	−300.9	−5.6	88.9	2	14.3	140.8	−1.2	144.8	4
Latitude:Longitude	11.9	−124.3	−5.2	95.7	1	18.2	−275.5	−7.0	956.9	1
Random Effect: Bloc	7.3	−358.3	−2.1	36.6	4	9.5	486.1	−3.6	496.4	2

* In the forest dataset, distance to market correlated with population pressure (>0.7) and water deficit (>0.5), but was a poorer predictor than either, so it was excluded from the full model (Table 1). EDF: Estimated Degrees of Freedom; ΔGCV: change in Generalised Cross-Validation score; ΔD$_2$: change in percentage of Deviance explained; ΔAIC: change in Akaike's Information Criterion score.
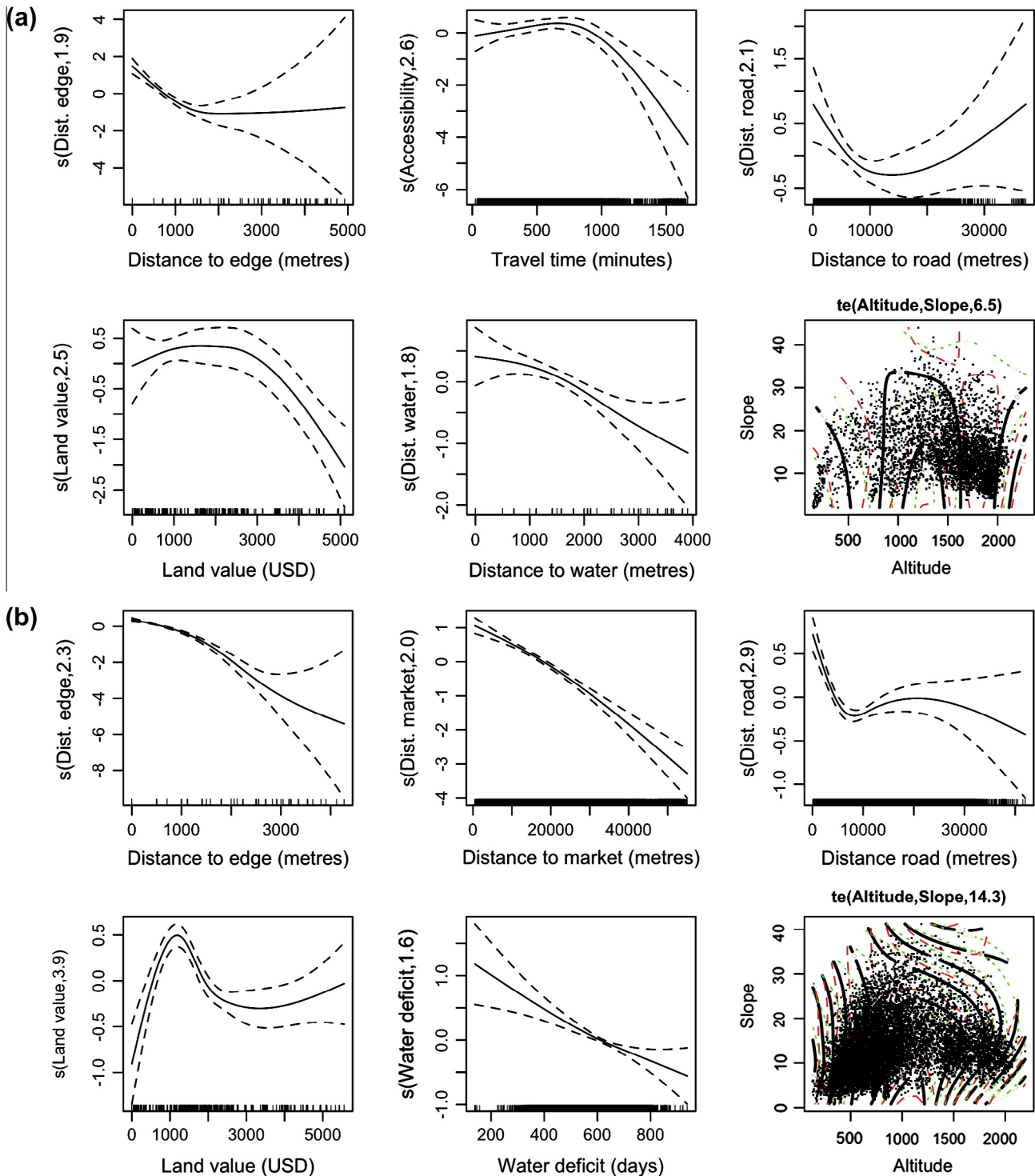
Fig. 2. The relationships between continuous predictors and habitat conversion are plotted (solid lines) for forest (a) and woodland (b). Dashed lines indicate approximate 95% confidence intervals.

scale conversion for subsistence agriculture (Fisher, 2010). Our spatially explicit models found that forest and woodland loss is well predicted by relationships with local socio-economic factors, particularly accessibility. For forest, highest conversion rates are found at mid elevations with low ruggedness, suggesting that topographic accessibility and potential for farming could be important considerations. However, there are also topographically-accessible locations where levels of forest loss have been relatively low. Whilst counter-intuitive, this could be explained if the

remaining forests in these locations are subject to some other limitation. For example: they may have already been heavily utilised for timber so that high value species are largely absent (Ahrends et al., 2010); they may occur in areas unsuited to agriculture (karst limestone for example); or they may have protection from local communities.

For woodland, habitat loss is highest at low and mid-elevations in relatively flat areas. Above an elevation of around 1100 m, the likelihood of woodland loss decreases sharply. Again, this could
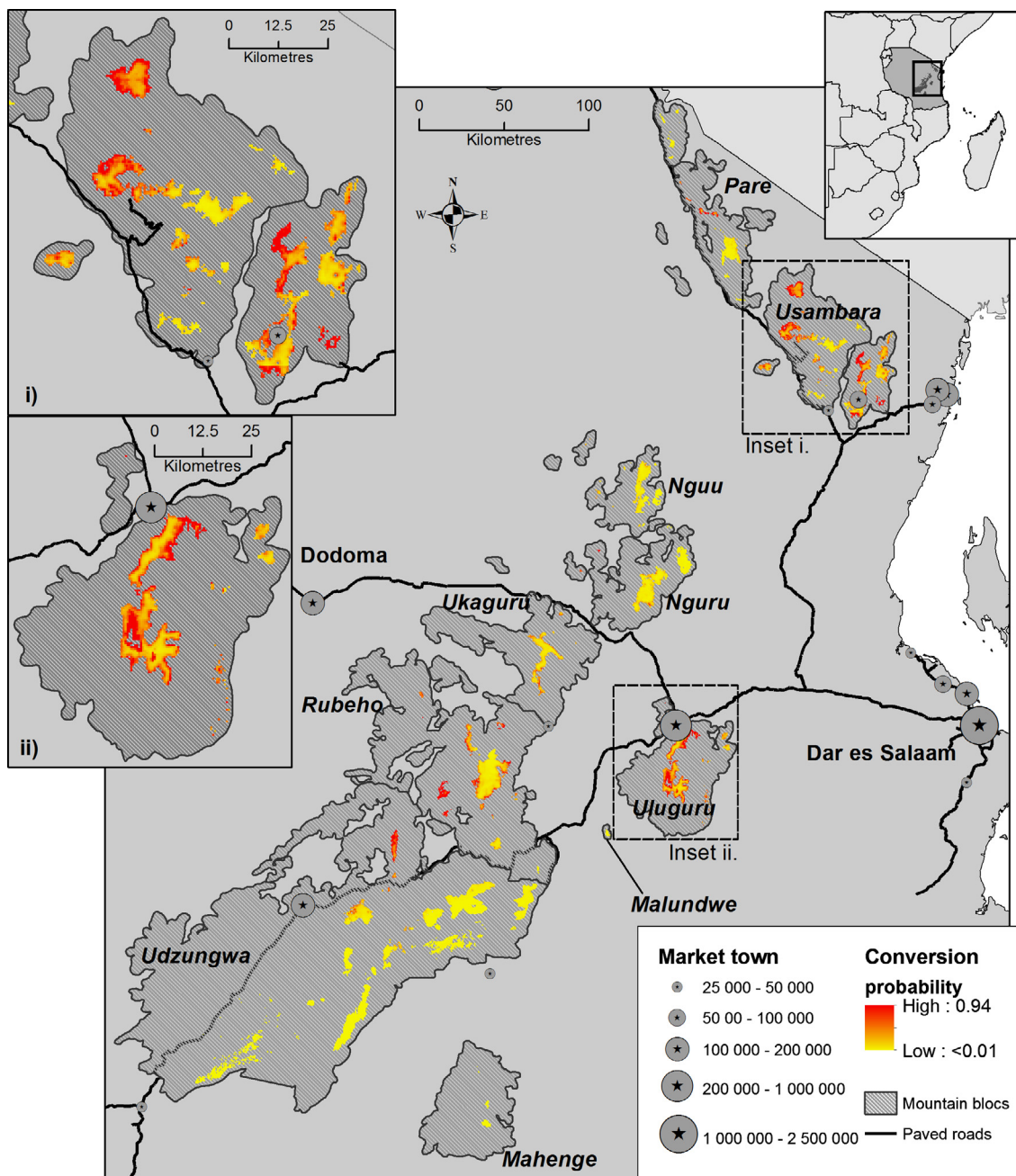
Fig. 3. Annual probability of forest (a) and woodland (b) conversion across the Eastern Arc Mountains. Predictions are based data for the year 2000 and are only mapped for pixels that are 50% forested in that year. Insets show close up of Usambara (i) and Uluguru (ii) Mountains. Locator map shows location of Tanzania and the Eastern Arc Mountains within East Africa.

be due to a number of reasons. For instance, there is less woodland at higher altitudes, perhaps making it less worthwhile to invest time and resources in charcoal production. In addition, trees in high altitude woodland may be smaller and it is likely that transporting harvested goods, especially charcoal bags to markets in the lowlands, becomes harder if routes cross rugged mountain terrain. For both forest and woodland, the strong relationship with distance to habitat edge also highlights the danger of increased fragmentation of forests, which may greatly increase levels of threat.

Although factors affecting habitat loss are complex and operate across multiple spatial and temporal scales (Geist and Lambin, 2002), our study has found similar results to those reported in other regions of the world. For example, topography was found

to be an important predictor of habitat loss in Brazil, Thailand and East Africa (de las Heras et al., 2012; Patarasuk and Fik, 2013 Pfeifer et al., 2012) and distance to roads and towns is amongst the most frequently cited predictors of forest loss in spatially explicit deforestation models (e.g. Chomitz and Gray, 1996; Mann et al., 2010; Patarasuk and Fik, 2013; Pfeifer et al., 2012). Whilst we were unable to test for the effect of broad scale socio-economic changes and access to export markets that are important drivers of habitat loss in South America and Asia (e.g. DeFries et al., 2010; Müller et al., 2012), their influence is lower in Africa (DeFries et al., 2010). However, with issues of food security an increasing priority for national governments, the extent to which rates of habitat loss in Africa will respond to teleconnections with global agricultural markets, as found between Amazonian forest loss and interna-
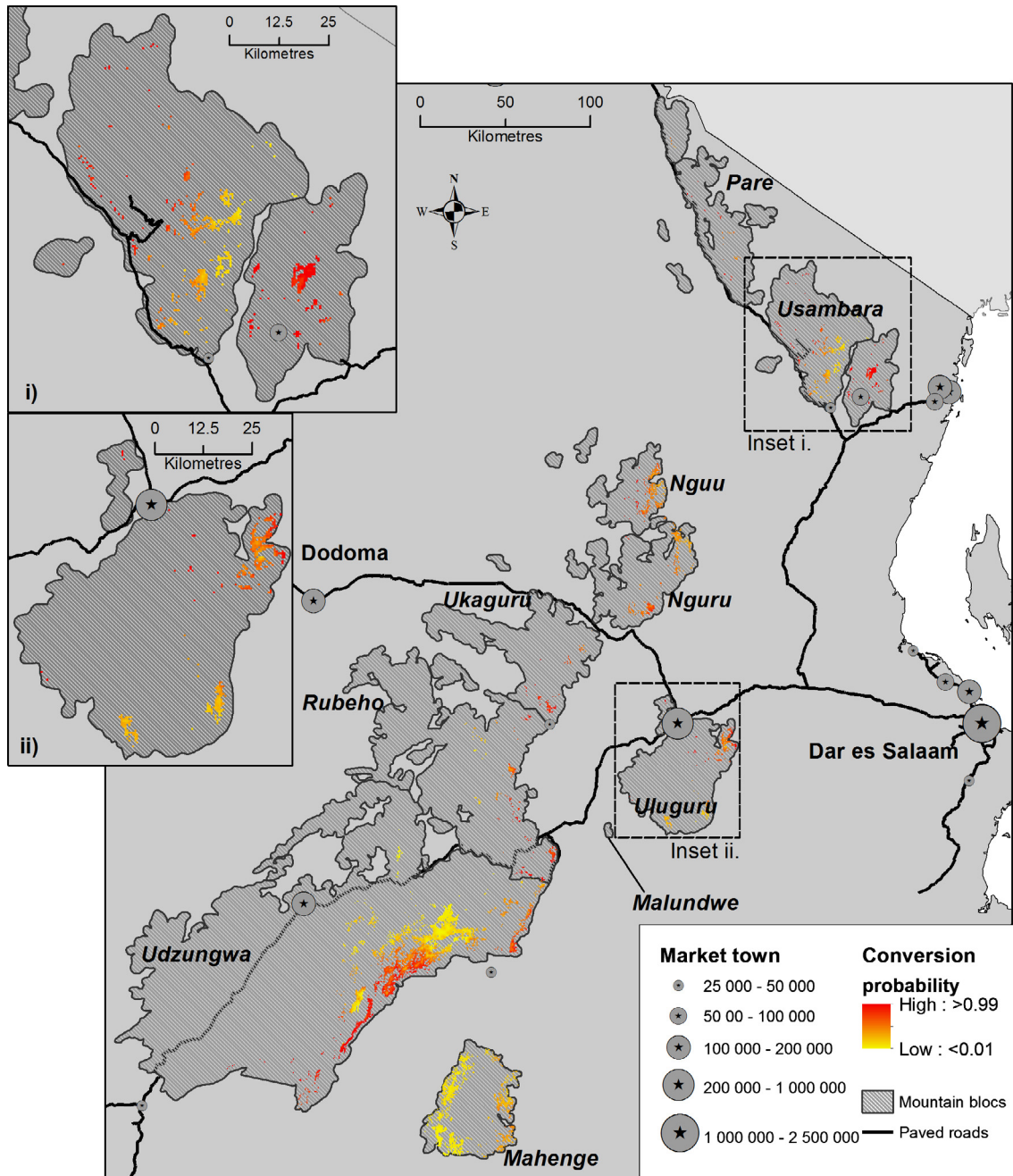
Fig. 3 (*continued*)

tional beef and soybean markets (Nepstad et al., 2006) remains to be seen.

As demonstrated by Pfeifer et al. (2012) observed rates of habitat loss are lower in protected areas than outside. More importantly, however, the observed rates inside protected areas are also lower than our models indicate would be expected in the absence of protection. This finding also corroborates a recent global systematic review of protected area effectiveness, which reports that, although absolute habitat loss within protected areas continues, the majority of protected areas are effective at reducing its rate (Geldmann et al., 2013). In the past half century, probably the most notable deforestation event in the Eastern Arc followed the degazettement of Shume-Magamba forest reserve in 1963 (Hamilton and Mwasha, 1990; Hurst, 2003). This degazettement was enacted due to the high local demand for land and ensuing

political will to meet this need. This event serves to highlight two things: first, the effectiveness of the forest reserve's protection status prior to degazettement and, second, the level of demand for agricultural land and its potential as a driver of habitat loss into the future.

Habitat loss is, however, still occurring within protected areas and effectiveness at reducing woodland loss is particularly low: protected areas reduce the expected conversion rate by just 16%. Our estimate of 40% effectiveness for forests is low globally but typical for Africa (Carranza et al., submitted for publication); however, an effectiveness score of just 16% for woodland is very low compared to other estimates for this region. As habitat fragmentation continues and as protected area boundaries become "habitat edges", our models also suggest that threat is likely to increase. It is possible that we have underestimated protected area effective-

ness, because we assigned areas as protected, or not, based on their status in 2000, so even if an area was not gazetted until 1999, the loss it incurred over 25 years was nevertheless attributed to a protected area. However, this effect is likely to be minor: the vast majority of the Eastern Arc's protected areas were gazetted during colonial times, prior to 1975 (Haule et al., 2002). There are several recent examples where the protection status of reserves has been upgraded, but very few examples of new protected areas being added to the network (Burgess et al., 2007b; Newmark, 2008).

In developing biodiversity conservation plans for the region, the forests of the East and West Usambaras, the Ulugurus and the Rubehos are predicted to be the most threatened. This is a particular worry for almost 450 km^2 of unprotected forest that they hold between them. These four blocs (particularly the Usambaras and Ulugurus) are also amongst the most biodiverse of the mountain chain, hosting at least 23 vertebrate species endemic to just a single mountain bloc (Burgess et al., 2007a; Platts et al., 2010). The Udzungwas, also of high biodiversity importance, show a high level of threat to the woodland along their southeastern edge. This area is important for animal movements between forest patches (Jones et al., 2009) and lies adjacent to the highly fertile Kilombero floodplain. Our analyses also highlight the particularly high rates of woodland loss in the South Pares, East Usambaras, Ukagurus and Rubehos.

Conservation efforts in the Eastern Arc have historically focused on the forests, due to their biodiversity. However, an increased focus on the value of woodlands seems desirable, for four reasons. First, the majority of woodland lies outside protected areas. Second, the effectiveness of protected areas at reducing woodland loss is noticeably poorer than for forests, perhaps because greater recognition of the importance of forests to biodiversity conservation has led to greater management effort. Third, both inside and outside protected areas, rates of woodland loss are considerably higher than those for forests. Fourth, although woodlands may harbour lower biodiversity than forests, they play a critical role in generating ecosystem services and in the maintenance of ecological processes, such as large mammal migrations (Green, 2012; Jones et al., 2009). Further teasing apart the drivers of forest and woodland loss and investigating the effectiveness of current conservation strategies is of great practical importance in developing effective conservation strategies for a region of national significance for ecosystem service provisioning and global significance for biodiversity conservation.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.04.016.

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