Forest fragment spatial distribution matters for tropical tree conservation

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ABSTRACT

Deforestation and associated forest fragmentation are main drivers of species loss across the tropics. Many studies have focused on how fragment edge effect, size, isolation and shape, affect species persistence within landscapes. Little attention has been paid to the impact of the distribution of the fragments itself on the preservation of local species pools. Here we test the importance of the spatial distribution of remaining forest fragments, relative to other fragmentation effects, on tree species diversity, composition and rarity patterns within a tropical landscape converted to rubber plantations in southern Yunnan, China. We find that the remaining forest fragments are non-randomly distributed in the landscape, with most fragments located at higher elevations, steeper slopes and shade aspects. At the same time we find that most of the observed patterns in tree diversity, composition and rarity are explained by the location of the fragments within the landscape, with very little additional impact of other fragmentation effects, even though fragmentation started more than two decades ago. We conclude that during the initial stages of land use change, the protection of forest areas along the entire environmental gradient should be a prime focus for conservation efforts as it is at this stage that most tree species can be preserved in the landscape. We also stress the importance of small forest fragments for the conservation of tree species, especially because such fragments are usually located in sites with the highest deforestation rates.

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1. Introduction

Land use change is considered a main driver of biodiversity loss all over the world (Foley et al., 2005), especially for large-bodied mammals, birds and late successional trees, and can cause rapid ecosystem decay and loss of ecosystem services (Laurance et al., 2002; Terborgh et al., 2001). However, many studies also show that remnant forest fragments can still maintain high phylogenetic diversity (Arroyo-Rodriguez et al., 2012; Mo et al., 2013), harbor a large proportion of original species (Arroyo-Rodriguez et al., 2009; Sodhi et al., 2010), has almost no effect on certain groups of taxa (Andreazzi et al., 2012), while some groups even increase their abundance and diversity (Crooks and Soule, 1999). Such contrasting outcomes of fragmentation are related to how much original forest remains after fragmentation, the size and isolation of individual fragments and the distribution of the fragments over the landscape (Laurance et al., 2002; Pardini et al., 2010; Prugh et al., 2008). For example, lowland forests in Jamaica were cleared

at a rate seven times higher than that of montane forests (Chai and Tanner, 2010), leading to disproportionate loss of lowland forest and associated taxa. Similarly, forests fragments with high fruit availability can maintain high avian diversity regardless of the patch isolation and size, but since these fragments are generally located on more fertile soils they are also prime targets for agricultural expansion and thus tend to become rare in fragmented landscapes (Garcia et al., 2010).

In the past 30 years studies in forest fragments focused mostly on impacts of patch size, isolation and edge effects on forest structure, species diversity and composition (Laurance et al., 2002, 2011). However, forests, and especially tropical forests, show strong spatial and environmental structuring of species composition and diversity (Baldeck et al., 2013; Garcia-Lopez et al., 2012; Harms et al., 2001; John et al., 2007; Laurance et al., 2010), meaning that the distribution of the fragments itself will, for a large part, determine the type and diversity of taxa preserved across the landscape (Virgos, 2001). Since forest fragmentation is generally a non-random process, with people targeting areas that are easily accessible or have good soil properties for agricultural production, forest fragments are usually restricted to areas located on steep slopes, poor soils or with inaccessible topography (Summerville and Crist, 2004; Vellend et al., 2008). The spatial distribution of

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forest fragments across the landscape may therefore form a major, but understudied, driver of species loss in fragmented landscapes (Mortelliti et al., 2010; Seabloom et al., 2002).

Tropical Asia is experiencing some of the highest deforestation rates observed across the tropics because of the rapid expansion of mono-culture cash crops such as rubber and oil palm (Koh and Wilcove, 2008; Mann, 2009; Sodhi et al., 2010), resulting in massive forest loss and fragmentation (Gibbs et al., 2010; Mantyka-Pringle et al., 2012). In this study we focus on the role that the spatial distribution of remaining forest fragments play in the preservation of tree species across a tropical landscape in southern China. This area is experiencing a rapid expansion of rubber plantations at the expense of the original tropical forest that used to cover the whole region until a few decades ago (Hu et al., 2008). We hypothesize, based on observations in fragmented landscapes mentioned earlier, that this expansion of rubber plantations is spatially non-random and will result in remaining forest fragments being located on less accessible, steeper, higher and shady slopes. Due to the relatively recent start of forest fragmentation in the study area compared to the long lifespan of trees and the embedding of the fragments within an 'artificial' forest landscape, we hypothesize that tree diversity, rarity and composition patterns in forest fragments will be more related to fragment location than to forest degradation related to fragment size and edge effects.

2. Methods

2.1. Study area

All studied forest fragments were located within a 20 km-diameter circle around the Xishuangbanna Tropical Botanical Garden in Menglun town, Mengla County, Xishuangbanna Dai Autonomous Prefecture, Yunnan Province, China (Fig. 1). Xishuangbanna is located on the northern edge of tropical Southeast Asia and it has the largest area of tropical rainforest in China. In addition, it lies within the Indo-Burma biodiversity hotspot (Myers et al., 2000) and has a native flora of ∼3500 plant species (Zhu, 2012). In our study area the average annual temperature varies around 21.5 °C

and rainfall around 1563 mm per year, with ca. 80% of the rain falling in the rainy season between May and October (Cao et al., 2006). The topography is characterized by steep slopes with altitudes ranging from 400 to 1460 m. The soils consist mainly of three types: laterite soil, laterite red soil and limestone-derived soil, each with specific forest types (Cao et al., 2006). While the tropical seasonal moist/monsoon forests in the area harbor the highest plant diversity, forests on limestone are characterized by high levels of endemism because of their unique soil and micro-climatic environments (Clements et al., 2006).

Originally, most of the study region was covered by forest; however, rubber plantations have recently become the main driver of habitat loss and fragmentation (Aziz et al., 2010; Hu et al., 2008). Before the 1980s the area was minimally exploited and forests well protected. Today, the landscape around Menglun consists for more than 64% of rubber plantations and about 25% natural forest, most of which is located in isolated patches varying in size, shape and isolation. There are three nature reserves in the area, although parts of the reserves are disturbed because they were used for growing *Amomum* (a ginger) in the forest understory (Hu et al., 2008). Since rubber expansion is the sole cause of forest conversion in this region, all forest fragments are surrounded by a similar vegetation matrix of evenly spaced rubber (*Hevea brasiliensis*) trees.

2.2. Land use classification

For the land use classification we used images from the Global Land Survey (GLS) dataset, which were downloaded from the International Science Data Service Platform (http://datamirror.csdb.cn/gls/glsLook.jsp). We georeferenced the GLS-2010 image using the GLS-2005 image (which was already orthorectified) using ERDAS IMAGINE AutoSync and used a gap-filled Digital Elevation Model (DEM) from the Shuttle Radar Topography Mission (SRTM) to account for relief displacement. Root mean square error for the georeferencing was less than 0.5 pixels (15 m). We then applied a supervised maximum likelihood classification method to the GLS-2010 image. Large homogeneous areas were selected from Google Earth to serve as training areas for the GLS-2010
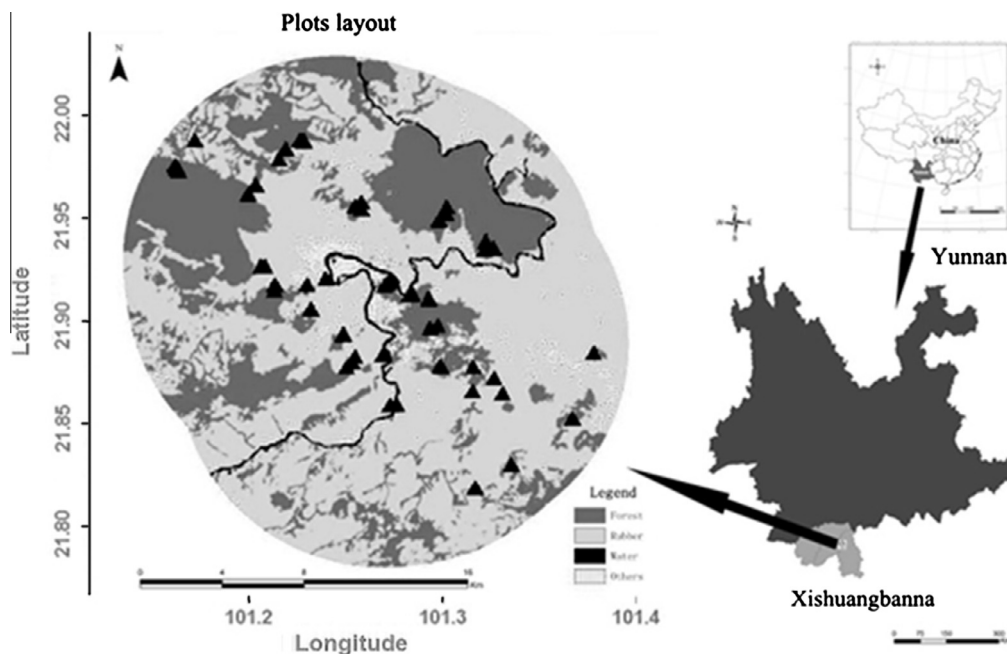
Fig. 1. The geographical location of the 50 plots in China (upper right), Yunnan Province (lower right) and the study area (left). Light gray in the left pannel indicates rubber plantations, dark gray the forest fragments. The fifty plots are indicated by black triangles.

classification. For each land-cover class at least 10 training areas were selected to reflect the variation due to topography and growing conditions. The thematic image was classified into four different classes: natural forest, rubber plantation, water, and others. We did another round of manual editing by visual interpretation on the classification results with the help of high resolution images from Google Earth and thematic maps from Hu et al. (2008). The resolution of the resulting classified map was 30 × 30 m (Fig. 1).

2.3. Natural forest and rubber plantation distribution patterns

To determine the environmental and spatial distribution patterns of natural forest (hereafter known as forest) and rubber plantations, we extracted the elevation, slope, and aspect data from the International Sciences Data Service Platform (http://datamirror. csdb.cn/list.dem?opType=list&type=gdem) for each 30 × 30 m grid cell in our land-use map. Based on this we calculated the proportion of grid cells classified as rubber and forest for elevation, slope and aspect categories using the software *Fragstats version 4.0* (http://www.umass.edu/landeco/research/fragstats/fragstats. html), which is a spatial pattern analysis program for raster maps.

2.4. Forest fragment tree surveys

A priori, we selected 50 forest sites that covered a wide range of environmental conditions (elevation, slope, aspect) and fragment sizes using our land use classification map. Sixteen of the 50 sites were located within nature reserves and, as far as possible, covered the same wide range of environmental conditions as the fragment plots. At each of the 50 selected sites we established a tree survey plot consisting of circular subplots (5 m diameter each) which were spaced at ten meter intervals along a transect that followed the length of the fragment for narrow elongate fragments or the elevation isoclines if fragments were larger. The number of subplots varied per plot because we added subplots to each transect until a minimum of a hundred stems (diameter at breast height [dbh] ⩾ 1 cm) were included. We used this variable area approach because fixed area sampling can result in considerable differences in included stem numbers between plots which complicate species diversity and composition analyses (Slik et al., 2011). The smallest fragment size included in this study was determined by the requirement that all subplots had to be placed at least ten meters from the forest edge. Within each circular subplot we tagged, measured the diameter and identified all trees in the field. A voucher for each species was also collected in each subplot for cross-checking the field identification with herbarium material present in the herbarium of XTBG (HITBC). The vegetation inventory lasted from June 2012 to March 2013.

2.5. Species composition and diversity variables

We used detrended correspondence analysis (DCA) to compare the floristic similarity between the fifty plots using the *Vegan* package with "decorana" function in R (R Development Core Team 2012). The first DCA axis was used as our measure of species composition similarity between plots because this axis represents the main floristic gradient. For species diversity we used the number of tree species we found in our standard samples of 100 stems per plot. Additionally we defined rare species as those with less than or equal to five individuals in the total inventory data set of 5000 stems, and then counted the number of stems belonging to these rare species in each plot as a measure of abundance of rare species.

2.6. Environmental and fragmentation variables

To disentangle the respective roles of fragmentation effects and fragment location on observed species diversity, rarity and composition patterns (the response variables), we included both fragmentation and environmental data as explanatory variables in our model selection. The environmental variables included: slope and elevation, with plot values based on the average values of the individual subplots; disturbance (e.g. logging and/or ginger plantation) as 0 when absent and 1 when present; limestone outcrops (if visible limestone rocks near or in our forest sites were detected) as 0 when absent and 1 when present; topographical position, with valley (lower quarter of a hillside) classified as 0, slope (the intermediate slope positions) classified as 1, and ridge (upper quarter of a hillside) classified as 2; aspect as 0 for plots facing 91–359 degrees and 1 for sites facing 0–90 degrees; and finally presence inside (1) or outside (0) of a reserve. The fragmentation variables included: distance of each plot to the nearest forest edge (shortest projected horizontal distance); fragment size in which the plot was located (log10 transformed surface area) and the fragment perimeter(log10)/size(log10) – ratio. Since most rubber forests were planted at similar time, fragment age was not included as an environmental variable. Because our plots differed in sampled surface area, we also added number of subplots sampled per plot as an explanatory variable to our analysis. All fragment metrics were based on our forest classification map and calculated using *Fragstats version 4.0*.

2.7. Statistical analyses

To test to what extent species composition, diversity and rarity (response variables) in our fifty plots were affected by fragmentation and/or their location we applied multiple linear regression techniques using the software 'Spatial Analysis in Macroecology' (SAM) version 4.0 (Rangel et al., 2010). Since species diversity and rarity were count variables, we first tested whether they conformed to normal distributions. Species diversity was normally distributed, but species rarity had to be square root transformed to make this variable normal. We subsequently checked the Variance inflation Factors (VIF) of each predictor variable in the full models to determine whether multicollinearity of variables formed a problem. All VIF values were below four, suggesting that collinearity of variables did not affect our results. Finally we tested whether our response variables (species composition, diversity and rarity) were spatially autocorrelated using Moran's I since spatial autocorrelation is known to affect model selection (Quesada et al., 2012; Slik et al., 2013). This showed that all of our response variables had significant short distance spatial autocorrelation. To account for this spatial autocorrelation we calculated eigen-vector based spatial filters as applied in the software package 'Spatial Analysis for Macroecology (SAM) version 4.0. This method extracts spatial filters using the Principal Components of Neighbour Matrices: PCNM (Brocard and Legendre, 2002).

We then proceeded with the model selection procedure by calculating ordinary least square (OLS) linear multiple regression models based on each possible combination of predictor variables and ranking these according to their Akaike Information Criterion with a correction for finite sample sizes (AICc). We included the spatial filters as fixed predictor variables to this model selection procedure to account for the spatial autocorrelation in our response variables. Our objective was not to find the single best predictive model for the response variables, but to explore the strength and direction of the predictor variables across all models using a model averaging approach based on the Akaike Information Criterion weights (AICc-wi). AICc-wi represents the likelihood of a given model relative to all other models and thus varies between

zero and one (Wagenmakers and Farrell, 2004), with the model with the lowest AICc having the highest AICc-wi. Model parameters were averaged across all models and weighted by their AICc-wi. A one tailed *t*-test was used to determine whether the variation in regression coefficients observed for each variable across all models differed significantly from zero. Additionally we calculated the importance value of each predictor variable. The importance value of a predictor variable is calculated by simply adding the AICc-wi values of the models in which the variable was present, i.e. if variables were present in the most likely models they will have a high importance value. Importance values vary between zero (low importance) and one (high importance).

To determine the individual and shared contributions of the environmental, fragmentation and/or spatial variables on our response variables we performed partial correlation tests, whereby we split our explanatory variables into separate groups (environment, fragmentation, space). For each response variable this analysis was performed for all models with a delta-AICc < 2, after which partial regression results were averaged. This analysis was also performed with SAM version 4.0.

3. Results

3.1. Non-random distribution of forest and rubber plantations

The total area occupied by rubber plantations in our study area was twice (310.2 km^2) as large as the forest area (154.0 km^2), with most of the forest heavily fragmented into smaller pieces (396 patches) but rubber plantations forming a more continuous and connected vegetation cover surrounding the forest fragments (Figs. 1 and 2). Most of the remaining forest fragments were small and had a large perimeter/area-ratio (Figs. 1 and 2). Rubber plantations were located at lower elevations (797 [MEAN] ± 198 [SD] m) than forest fragments (894 ± 215 m) (Wilcoxon two sample test, *p* < 0.001), with rubber plantations having replaced most forests at the lowest elevations (Fig. 3). Forest fragments were also significantly more often found on steeper slopes (18.5 ± 8.6°) than rubber plantations (16.5 ± 8.2°) (Wilcoxon two sample test, *p* < 0.001), where they disproportionally faced northern to eastern aspects with lower illumination, especially during winter (Fig. 3).

3.2. Fragmentation versus environmental drivers of biodiversity

In total, 420 species were found in our 50 plots with a mean of 27.9 ± 12.1 species in each plot. Species richness ranged from three

species found on a ridge top of a limestone forest, to a maximum of 51 species found in the valley of a non-limestone forest. Species composition differences were strongly loaded along the first DCA-axis (40.2% of data variance), which mainly separated forests on limestone from non-limestone forests.

The regression models explained considerable amounts of data variance for species diversity (R^2 = 0.743), species composition (R^2 = 0.837) and abundance of rare species (R^2 = 0.551) (Table 1). Most of this explained variation was due to environmental rather than fragmentation and/or spatial variables (Table 1 and Fig. 4). Species richness was mostly affected (high Importance value [IV]) by presence of limestone (negative), topography (negative, i.e. decreasing upslope), disturbance (positive), presence in nature reserve (positive), aspect (positive, i.e. more diverse in shade aspects), slope (negative), and fragment size (negative) (Table 1). Species composition was strongly associated (high IV) with presence of limestone outcrops, topography, disturbance, elevation, and slope (Table 1). The abundance of rare species was mostly affected (high IV) by topography (declining upslope), presence in forest reserves (positive), and fragment size (negative) (Table 1).

4. Discussion

4.1. Drivers of tree species diversity, composition and rarity

Our regression models were able to explain 55%, 74% and 84% of the respective variation in species rarity, species richness and species composition across our study area. This signals the importance of the environment in shaping the distribution and abundance of tree species in this landscape. An important reason for these high percentages explained data variance can be linked to the strong environmental gradients found in our study area, both in elevation and soil types, as this is shown to influence the strength of tree species habitat associations (Punchi-Manage et al., 2013). The main driver of species compositional turnover was linked to the transition from limestone to none-limestone soils. On the limestone soils only a limited set of tree species were found which also explains the negative correlation between limestone and species richness. In some limestone plots up to 80% of individuals belonged to just two species, namely *Cleistanthus sumatranus* (Miq.) Muell. Arg. (Phyllanthaceae) and *Lasiococca comberi* Haines (Euphorbiaceae). This in stark contrast to forests on none-limestone soils which could be highly diverse with up to 51 tree species per 100 stems. This contrast is most likely related to the harsh conditions in the
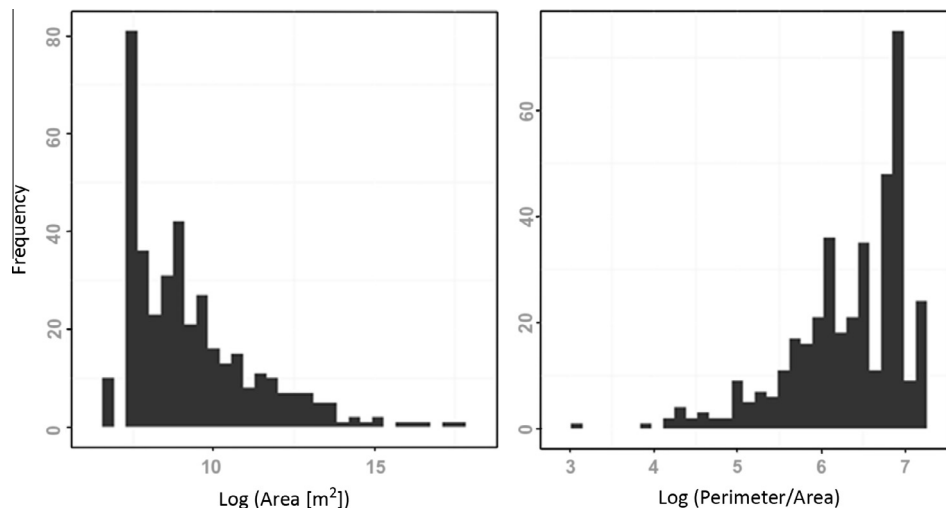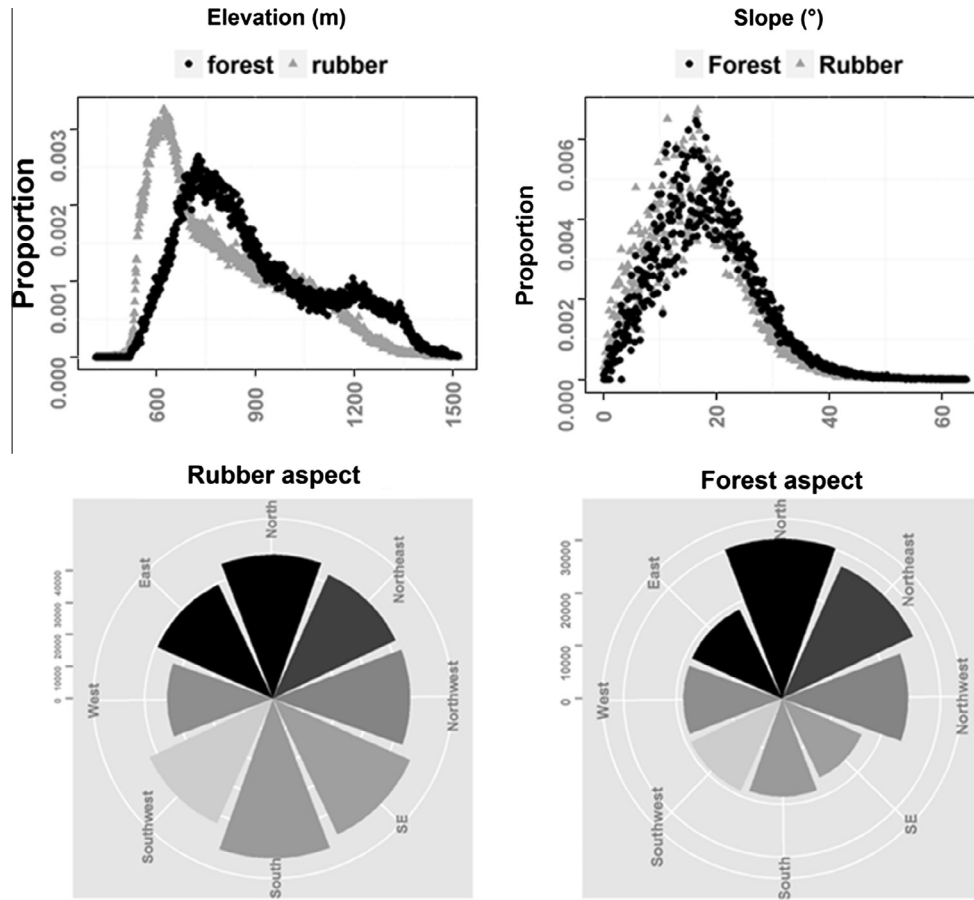

Fig. 2. Frequency distribution of log transformed forest fragment sizes (left panel) and their log transformed perimeter/area distribution (right panel) in the study area, showing that most forest fragments were small and had high perimeter to area ratios.

Fig. 3. The landscape parameters of forest fragments and rubber plantations showing that forest fragments were displaced by rubber plantations at lower elevations (upper left panel); located at steeper slopes (upper right panel); and disproportionally located at low illumination northern and eastern aspects (lower two panels) compared with rubber plantations.

Table 1
Variables explaining changes in observed tree species richness, composition and rarity in forest fragments. Standardized regression coefficients (SRC) represent AIC-wi weighted averages, with significance levels (*0.05 < p > 0.01; **0.01 < p > 0.001; ***p < 0.001) indicating whether the mean SRC deviated significant from zero. The importance value (IV) represents the sum of the AIC-weights of the models in which a variable was selected, ranging from 0 to 1 (0 is low support, 1 is maximum support). Limestone = presence of limestone outcrops; Topography = valley (0), mid slope (1) or ridge (2); Disturbance = absent (0), present (1); Forest reserve = outside (0), inside (1); Aspect = 91–359 degrees (0), 0–90 degrees (1); Fragment size = log10 transformed fragment surface area of fragment; P/A-ratio = log10 transformed fragment perimeter length divided by log10 transformed fragment surface area; Edge distance = horizontal distance to the nearest forest edge; Sample = number of subplots per plot used for the tree species inventory (added to control for beta-diversity effects on the analyses); R^2 = proportion explained data variance; N = sample size.

Grouping	Variables	Species richness		Species composition		Species rarity	
		IV	SRC	IV	SRC	IV	SRC
Environment	Limestone	0.924	−0.313**	1.000	0.712***	0.297	−0.131***
	Topography	0.998	−0.427***	0.817	−0.204**	0.999	−0.534***
	Disturbance	0.578	0.226***	0.624	−0.162***	0.245	0.080*
	Forest reserve	0.670	0.300**	0.218	−0.058**	0.707	0.294**
	Aspect	0.601	0.173***	0.255	0.073***	0.479	0.179***
	Elevation (m)	0.380	0.153***	0.966	−0.249***	0.451	0.193***
	Slope (degrees)	0.518	−0.167***	0.652	0.156***	0.426	−0.176***
Fragmentation	Fragment size	0.866	−0.335***	0.178	0.038*	0.736	−0.385**
	Edge distance	0.493	0.206***	0.325	−0.104***	0.222	0.069*
	P/A-ratio	0.433	−0.227***	0.192	0.055***	0.431	−0.257**
	Sample	0.313	0.127***	0.361	0.115***	0.280	0.124***
Space	Spatial filter 1	1.000	−0.315**	1.000	0.059	1.000	−0.281*
	Spatial filter 2	1.000	0.253	1.000	−0.066		
	Spatial filter 3			1.000	−0.111		
	R^2		0.743		0.837		0.551
	N		50		50		50

limestone areas during the dry season, which due to their low water retention capacity tend to dry out much earlier in the dry season than the none-limestone areas (Tang et al., 2011). Selection

for drought tolerant species is therefore strong, and both *C. sumatranus* and *L. comberi* are characterized by small stature and high wood densities (ca. 0.8 g cm^{-3}), indicating slow growth

Species diversity

Species composition
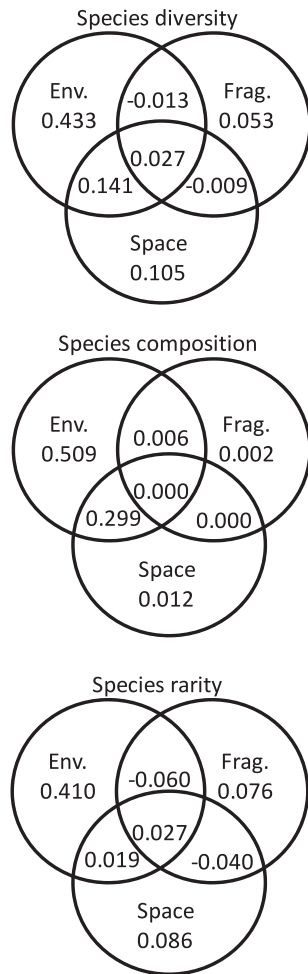
Species rarity

Fig. 4. Variance partitioning showing the individual and shared contributions of environmental, fragmentation and spatial variables on species diversity, composition and rarity. Values represent the average of models with a delta-AICc < 2 (n = 14, 8 and 15, for species diversity, composition and rarity respectively).

and well developed resistance to drought related vessel cavitation (Hacke et al., 2001). Given the general wood density of ca. 0.6 g cm^{-3} in our study area (Slik et al., 2013), most tree species will probably be incapable of long term survival in the limestone habitats.

Species richness and rarity variation showed overlap in explanatory variables, with both showing highest levels within forest reserves, in valleys, and oddly enough in smaller sized forest fragments. The positive effect of nature reserves on tree diversity and abundance of rare species seems to indicate that the additional protection provided in these reserves pays off in terms of tree species conservation. China's strict nature reserves are clearly delineated and little tree harvesting is taking place inside them, which may explain their relatively high tree diversity and abundance of rare species. Higher tree species diversity and rarity within forested valleys rather than ridges and hillsides is corroborated by many other studies in tropical forests (Baldeck et al., 2013; Harms et al., 2001; Laurance et al., 2010) and is probably linked to increasing water and nutrient availability at lower topographic positions, more stable climatic conditions during the dry season due to continued presence of soil water sources, and higher forest productivity and dynamics which may promote species coexistence due to the intermediate disturbance effect (Balvanera et al., 2003; Newbery and Gibbons, 2003). The negative correlation between forest patch size and tree diversity and rarity may be

related to the fact that small fragments are disproportionately located in the most productive sites, which were originally covered with the most diverse forest type. The observed negative correlation with forest patch size is thus more affected by fragment location than by forest degradation due to edge, size or isolation effects.

4.2. The importance of forest fragment spatial distribution for tree species conservation

Contemporary patterns in tree species diversity, composition and rarity in this tropical fragmented landscape in southwestern China, were overwhelmingly driven by the location of the fragments rather than by fragmentation effects, even though fragmentation in this area started more than two decades ago. An important reason for this lack of fragmentation impacts is likely related to the fact that the fragments are embedded in a forest plantation matrix which reduces the impact of edge effects (Laurance et al., 2011). Indeed, similar lack of edge effects was found in a Bornean old growth forest surrounded by a burned forest matrix (Slik et al., 2011). Since edge effects are generally considered to be among the most potent drivers of fragmented forest degradation, especially for small fragments (Laurance et al., 2002, 2011), any reduction in edge effect intensity will slow forest degradation considerably, meaning that these fragments can maintain their original species composition and forest structure longer than more exposed fragments. The lack of fragmentation effects in this study is also affected by the long life span of trees which can have generation times of centuries rather than decades, i.e. even in small fragments it can take a long time for most tree species to disappear (Helm et al., 2006; Vellend et al., 2006). This means that small forest fragments can initially maintain levels of tree diversity that are much higher than expected based on 'equilibrium' predictions from island biogeography, leading to an 'extinction debt' (Vellend et al., 2006). At the same time, forests in seasonal SE Asia have been subject to swidden agriculture and natural forest fires for thousands of years, and current species diversity and composition may reflect this (Chazdon, 2003; Fairhead and Leach, 1998; Mo et al., 2011), resulting in forests that are already quite resilient to fragmentation effects.

The lack of negative impacts of fragment size, plot distance from the forest edge and fragment perimeter/area-ratio, at least during the initial few decades, means that changes in tree species diversity, composition and rarity in this fragmented landscape are mainly determined by where the remaining fragments are located. To preserve the complete tree flora, including the relative abundances of the individual species, fragments should therefore be distributed evenly across the environmental gradients present in the area. However, we found strongly biased spatial distribution of forest fragments across these gradients, with disproportionately reduced forest area at lower elevations, sun exposed aspects, flat areas and shallow slopes. All of these factors were found to affect patterns in tree diversity, composition and rarity, supporting our initial assumption that changes in tree species relative abundances across this landscape are non-random due to spatially biased patterns of rubber plantation development towards areas with higher productivity and easy access (Nguyen, 2013). This is congruent with findings from other mountainous regions in the world, where areas located in the lowlands, which are generally characterized by high productivity, have been progressively deforested, while inaccessible forest areas in less productive locations remain relatively intact (Chai and Tanner, 2010; Garcia-Lopez et al., 2012; Mayaux et al., 2005; Vellend et al., 2008). The location of forest reserves generally follows the same pattern as the deforestation trends detected here, with most reserves located in remote, inaccessible sites, probably resulting in protection of a non-representative

sample of species for the whole region (Chai and Tanner, 2010; Margules and Pressey, 2000; Pressey et al., 2002; Scott et al., 2001).

These findings have important implications for tree conservation because it emphasizes that apart from forest fragment size and edge effects, the representative distribution of forest fragments across the landscape should be a prime focus for conservation efforts. Conservation efforts can be extremely effective if they can ensure that all habitat types, and thus most species, will be preserved in the landscape during the initial land use change phase. Because forest fragments can maintain their original tree species composition at least for several decades but probably much longer if well protected (Vellend et al., 2006), a well planned spatial distribution of forest fragments will ensure that most species remain present for future reforestation. Simple, but effective algorithms already exist for designing the spatially most effective strategy for striking a balance between land use development and biodiversity conservation (Ardron et al., 2010; Carvalho et al., 2010; Margules and Pressey, 2000; Possingham et al., 2000; Steward and Possingham, 2005; Wilson et al., 2006), although an important caveat for designing such optimum conservation strategies in many tropical countries remains the lack of spatially explicit species presence and abundance data. Fortunately, our study showed very high correspondence between a few simple to attain environmental variables (elevation, slope, aspect, soil type, convexity, and presence in or outside forest reserves) and species diversity, composition and rarity. This means that spatial conservation designs based on environmental variables may produce results very similar to those that are based on actual species survey data.

4.3. Conclusions

We show that during the initial stages of land use change, the protection of forest areas along the entire environmental gradient should be a prime focus for conservation efforts as it is at this stage that most tree species can be preserved in the landscape. Once such protection has been achieved, the long lifespan of trees will ensure that these fragments can serve as life rafts for many species for at least several decades, giving time to employ additional conservation strategies targeted at reducing edge effects, connecting remaining fragments into larger regional forest networks, reforestation using local native tree species, and wildlife conservation and/or reintroduction. We like to stress that our results show that even small forest fragments are critical for tree species conservation, especially as such small fragments are usually located in sites with the highest deforestation rates.

Acknowledgements

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