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Elevational Distribution of Adult Trees and Seedlings in a Tropical Montane Transect, Southwest China

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Montane habitats are characterized by high variation of environmental factors within small geographic ranges, which offers opportunities to explore how forest assemblages respond to changes in environmental conditions. Understanding the distributional transition of adult trees and seedlings will provide insight into the fate of forest biodiversity in response to future climate change. We investigated the elevational distribution of 156 species of adult trees and 152 species of seedlings in a tropical montane forest in Xishuangbanna, southwest China. Adult trees and seedlings were surveyed within 5 replicate plots established at each of 4 elevational bands (800, 1000, 1200, and 1400 m above sea level). We found that species richness of both adult trees and seedlings changed with elevation, showing a notable decline in diversity values from 1000 to 1200 m. Tree species composition also demonstrated distinct differences between 1000 and 1200 m, marking the division between tropical seasonal rain forest (800 and 1000 m) and tropical montane evergreen broad-leaved forest (1200 and 1400 m). The results suggested that soil moisture and temperature regimes were associated with elevational distribution of tree species in this region. We also observed that seedlings from certain species found at high elevations were also distributed in low-elevation zones, but no seedlings of species from low elevations were distributed in high-elevation zones. The increase in temperature and droughts predicted for this region may result in the contraction of tropical seasonal rain forest at lower elevations and a downhill shift of higher tropical montane tree species.

Keywords: *Environmental gradient; tree species distribution; tropical montane forest; climate change; China.*

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Introduction

Understanding species distribution along spatial and environmental gradients is one of the core aims of ecological and biogeographical research (Whittaker 1960; Itow 1991; Wolf 1993; Vazquez and Givnish 1998; Buckley and Jetz 2008). The elevational gradient encompasses multiple environmental gradients within very short geographic distances (Körner 2007), offering opportunities for investigating the distribution of species in response to changing environments (Lomolino 2001; Grytnes and McCain 2007; Körner 2007).

Elevational distribution of plants has been widely reported (eg Van Steenis 1984; Kessler 2000; Hemp 2006; Jones et al 2011; Martin et al 2011). However, the patterns of species elevational distribution vary depending on the study locations, because they are likely to be influenced by multiple factors, including human and natural disturbances (eg Pereira et al 2007; Angelo and Daehler 2013), biotic interactions (reviewed by Anthelme and Dangles 2012), edaphic variables (eg Sanchez et al 2013), topography (eg Bohlman et al 2008), moisture (eg Patten and Ellis 1995; Leuschner 2000; Oliveira-Filho and Fontes 2000; You et al 2013), and temperature (eg Vazquez and Givnish 1998; Salas-Morales and Meave 2012). It is therefore important to account for multiple factors that may be related to plants' distribution patterns along elevational gradients.

In response to recent climate change, many species have been observed to shift their distributional ranges (Parolo and Rossi 2008; Hillyer and Silman 2010; Chen et al 2011; Meier et al 2012). In general, tree species on montane gradients are predicted to shift their distributions upslope due to increased temperature (eg Feeley et al 2011). However, Crimmins et al (2011) suggested that tree species in California forests are likely to move downhill as increased precipitation may render drier, lower elevations more suitable for high-elevation

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cloud forest species. Ledo et al (2009) also found that the dryer conditions at low elevations led to the migration of tropical cloud forest to gullies and higher elevations with humid conditions. By measuring environmental factors and elevational distributions of species, future impacts of climate change on the diversity of local forests may be predicted.

Some studies have also examined elevational distributions of seedlings under forest canopy, which can indicate potential future changes of forest structure (Lenoir et al 2009; Vitasse et al 2012). Tree seedlings were found to migrate upslope at faster rates than their adult counterparts (Lenoir et al 2009). The distribution of seedlings is also considered to reflect changes in climatic factors (Vera 1997; Ross et al 2012; Marcora et al 2013).

The seedling assemblage plays a key role in forest regeneration (Teketay 1997; Li et al 2010; Bace et al 2012), and range extension of tree species may be indicated by seedling migration under climate change scenarios. However, the elevational distribution of tree seedlings may not be the same as those of adult trees. Seeds of some species may be distributed far from parent trees to other less suitable elevations and sustain their populations as seedling banks (Lenoir et al 2009). Those seedlings may mature and change the forest structure significantly when the habitat becomes more favorable due to climate change.

Most studies of tree and seedling migration have been carried out in temperate forests (eg Bansal and Germino 2010; Urbieta el al 2011), with very few reported from tropical forests (Rehm and Feeley 2013). This study aimed to help fill that gap with an investigation in Xishuangbanna Dai Autonomous Prefecture in southwestern China, an area rich in biodiversity across various types of seasonal tropical forests (Cao and Zhang 1997; Zhu et al 2006). A number of studies of forest species composition and assemblage structures have been conducted in this region (Wu 1980; Wu et al 1987; Zhang and Cao 1995; Cao and Zhang 1997; Zhu et al 2005; Cao et al 2006). In Xishuangbanna, vegetation below 800 m in elevation has been classified as tropical seasonal rain forest, vegetation between 1000 m and 1200 m as tropical montane rain forest, and vegetation between 1200 m and 1400 m as tropical montane evergreen broad-leaved forest (Wu et al 1987). However, this classification is based on the elevational distribution of adult trees, and the classification of seedlings has not yet been quantitatively described within this region.

We investigated changes in the composition of adult tree and seedling species along an elevational transect in this region to address the following questions:

1. What are the elevational species richness and composition patterns of adult trees and seedlings? Do adult tree and seedling species have the same range of elevational distributions?
2. How does the composition of tree species respond to variation in environmental factors (eg temperature and soil moisture) as a consequence of elevational change?
3. What are the potential effects of local climate change scenarios on the distribution of tree species in mountains?

Materials and methods

Study site

Xishuangbanna Dai Autonomous Prefecture (21°08′ – 22°35′N, 99°56′ – 101°50′E) borders Myanmar in the southwest and Laos in the southeast (Figure 1). The region has a mountainous topography, with mountain ridges running in a north–south direction and a southward decrease in elevation. It has a typical monsoon climate with distinct wet and dry seasons. Mean annual air temperature and rainfall are 21.8°C and 1493 mm, respectively. Approximately 80% of the annual rainfall occurs in the wet season, which lasts from May to October. The frequent occurrence of heavy fog in the dry season in the lower hills and valleys may assist the expansion of the northern limit of tropical rain forest to this region (Cao et al 2006).

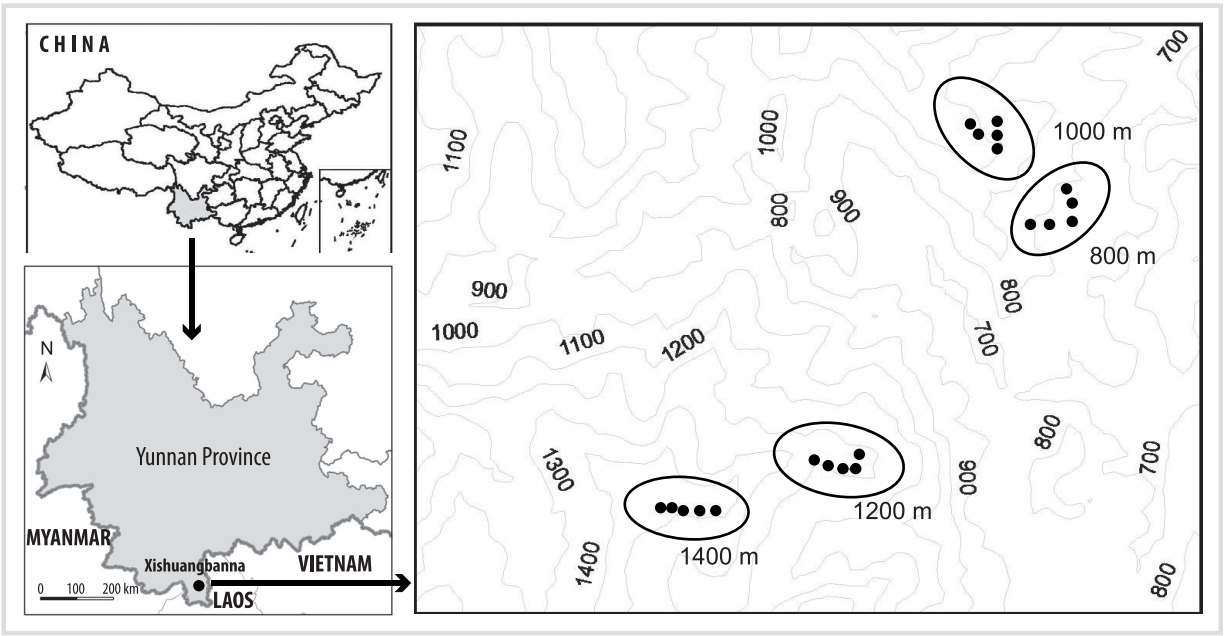
Data collection

In August 2012, we established a transect consisting of 4 elevational bands (800, 1000, 1200, and 1400 m above sea level—Figure 1 and Table S1, *Supplemental material*, http://dx.doi.org/10.1659/MRDJOURNAL-D-15-00109.S1). in the Xishuangbanna National Nature Reserve. Elevations below 800 m above sea level were not included in this study, as the forests were cleared or heavily disturbed. Within each elevational band, we set up 5 replicate plots of 20 m × 20 m that were spaced approximately 200 m from each other. Locations impacted by anthropogenic and natural disturbances, such as large canopy gaps, were avoided. Within each plot, all trees with a diameter at breast height ≥5 cm were measured and tagged. Most trees were identified on-site by local botanists; those that could not be identified were collected and brought back to Xishuangbanna Tropical Botanical Garden herbarium for further determination. In December 2013, five 1 m × 1 m subplots were established at the 4 corners and the center of each 20 m × 20 m plot to survey seedlings. Within each subplot, all stems of tree species <1 cm diameter at breast height (hereafter referred to as seedlings) were tagged and identified by species.

We recorded hourly temperatures from May 2013 to April, 2014 using a thermo-logger (DS1923 Hygrochron iButton, Maxim, CA, USA) set at the height of 1.3 m in the vicinity of each plot. Due to technical problems, no temperature measurements at 1200 m were made in July and August, and thermo-loggers at three 1000 m plots were lost during the dry season. We measured soil

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FIGURE 1 Location of 20 plots in 4 elevational bands (circled) in Xishuangbanna National Nature Reserve, southwest China. (Map by authors)



moisture at 5 cm below the ground at 5 randomly selected points within each subplot (a total of 25 measurements per plot) using a conductivity probe (Theta probe MPM-160B, ICT International Pty Ltd, Armidale, New South Wales, Australia) at the end of the wet (December 2013) and dry (April 2014) seasons. We used a geologic compass (HRB DQY-1, Harbin Optical Instrument Factory, Heilongjiang Province, China) to measure the slope and aspect of each plot.

Data analysis

The seedling data collected from the five 1 m × 1 m subplots in each plot were pooled before analysis. The abundances of the adult trees and the seedlings were log-transformed before calculating 3 species diversity indices: the Shannon-Wiener index, Simpson index, and Pielou evenness index (Magurran 1988).

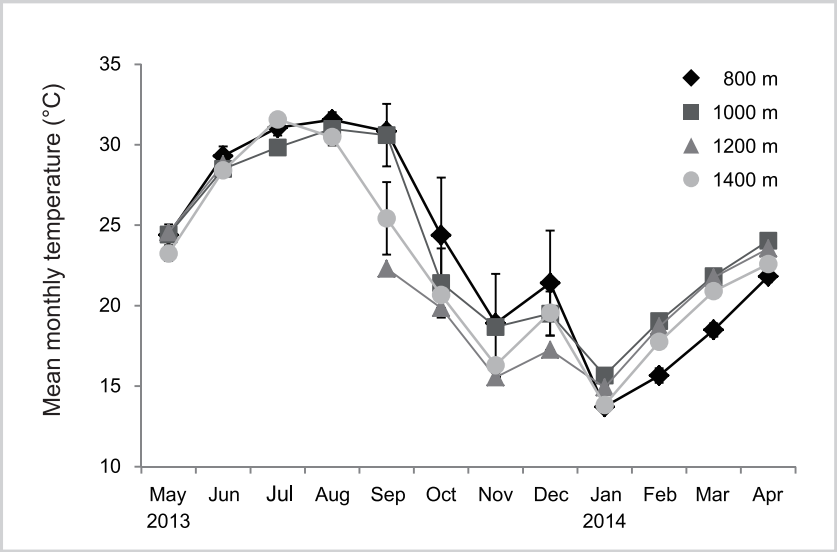
To test whether diversity and species richness differed in the different elevational bands, we used one-way analysis of variance (ANOVA) with post hoc Tukey's tests. Differences in assemblage composition were investigated using nonmetric multidimensional scaling (NMDS) ordinations with 10 random restarts (Minchin 1987), based on 4 types of similarity matrices: the Jaccard, Bray-Curtis (using log-transformed abundances), Chao-Jaccard (Chao et al 2005), and Raup–Crick (Chase et al 2011) indices. All species that occurred in 1 site only were removed before calculating similarity values to reduce overestimation of beta-diversity. Permutational multivariate analysis of variance (PERMANOVA) was used to test if the species compositions of adult trees and seedlings were significantly different among the 4 elevational bands (Anderson 2001; McArdle and Anderson 2001).

We adopted an information-theoretic approach (Burnham and Anderson 2002) to test whether assemblage composition of adult and seeding species was related to temperature, soil moisture, or other environmental factors, including elevation and geographic factors. We generated 12 environmental variables, which were grouped into 5 classes with similar attributes (temperature, soil moisture, elevation, topography, and spatial arrangement). For temperature data, we first calculated the average air temperature during the day (7:00 to 18:00 h) and at night (19:00 to 6:00 h) of each day in January–April (the dry season). These values were then used to calculate mean, maximum, and minimum air temperatures and their coefficient of variation. Wet season temperature data were not used due to the lack of data at 1200 m (explained earlier) and negligible differences between elevational bands in this season (Figure 2). Soil moisture measurements within each plot were averaged to generate wet-season (December) and dry-season (April) soil moisture and its seasonal variation. Topography consisted of slope and aspect measured within each plot. Spatial arrangement of the plots was quantified using the primary and secondary vectors of the principal coordinates of neighbor matrices (PCNM1 and PCNM2), which showed positive spatial correlation based on Moran's *I* (Dray et al 2006; Legendre and Legendre 2012).

We employed a model averaging method (Burnham and Anderson 2002) to investigate the relative importance of individual predictor variables in explaining variation in the composition of adult tree and seedling species. Using

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FIGURE 2 Mean monthly air temperature in the 4 elevational bands, May 2013 to April 2014. Data for the 1200 m band in July and August are missing (bars represent standard error).



multivariate generalized linear models developed by Wang et al (2012), we selected plausible predictor variables by testing whether the sum of the Akaike weights of each predictor variable was significantly greater than the summed Akaike weights obtained from a null distribution of the plots. The null model was generated by permuting plots (not individuals), as this preserved the tree species composition, and thus species interactions, of each plot. We compared the observed Akaike weights with those derived from 999 permutations. Due to the loss of temperature thermo-loggers from 3 plots at 1000 m during the dry season, we included only 17 plots (instead of 20) for the analysis using all 12 predictors. We then re-ran the same analysis using all 20 plots but excluding temperature predictors. Abundances were square-root transformed before analysis (Nakamura et al 2015).

To investigate differences (and similarities) in the elevational distributions of adult tree and seedling species, we used the indicator value protocol developed by Dufrêne and Legendre (1997), using the labdsv R package version 1.6-1. We calculated the indicator value of a given species for single elevational bands (eg 800 m, 1200 m) and all possible sequential elevational bands (eg 800–1000 m, 1000–1400 m) omitting the entire elevational range (ie 800–1400 m), giving a total of 9 indicator values per species. A random reallocation procedure with 4999 permutations was performed to test for the significance of indicator values. We selected the species with significant indicator values greater than 60% (a subjective benchmark value). We also calculated the importance value, which additively summarizes the relative abundance and the relative frequency of the selected adult and seedling tree species in each of the elevational bands (Curtis and McIntosh 1951).

Results

We recorded a total of 1034 adult trees (diameter at breast height $\geq$ 5 cm) representing 156 species from 103 genera and 51 families. A comparable number of seedlings (1105 individuals) were recorded, representing 152 species from 121 genera and 57 families. The most dominant adult tree species within each elevational belt were *Parashorea chinensis* at 800 m, *Alseodaphne petiolaris* at 1000 m, *Castanopsis echinocarpa* at 1200 m, and *Castanopsis mekongensis* at 1400 m. The most dominant seedling species were *Pittosporopsis kerrii* at 800 m, *C. echinocarpa* at 1000 m and 1200 m, and *Castanopsis calathiformis* at 1400 m. A large number of adult tree and seedling species were relatively rare, with distributions in only 1 elevational band (Tables S2 and S3, *Supplemental material*, http://dx.doi.org/10.1659/MRDJOURNAL-D-15-00109.S1

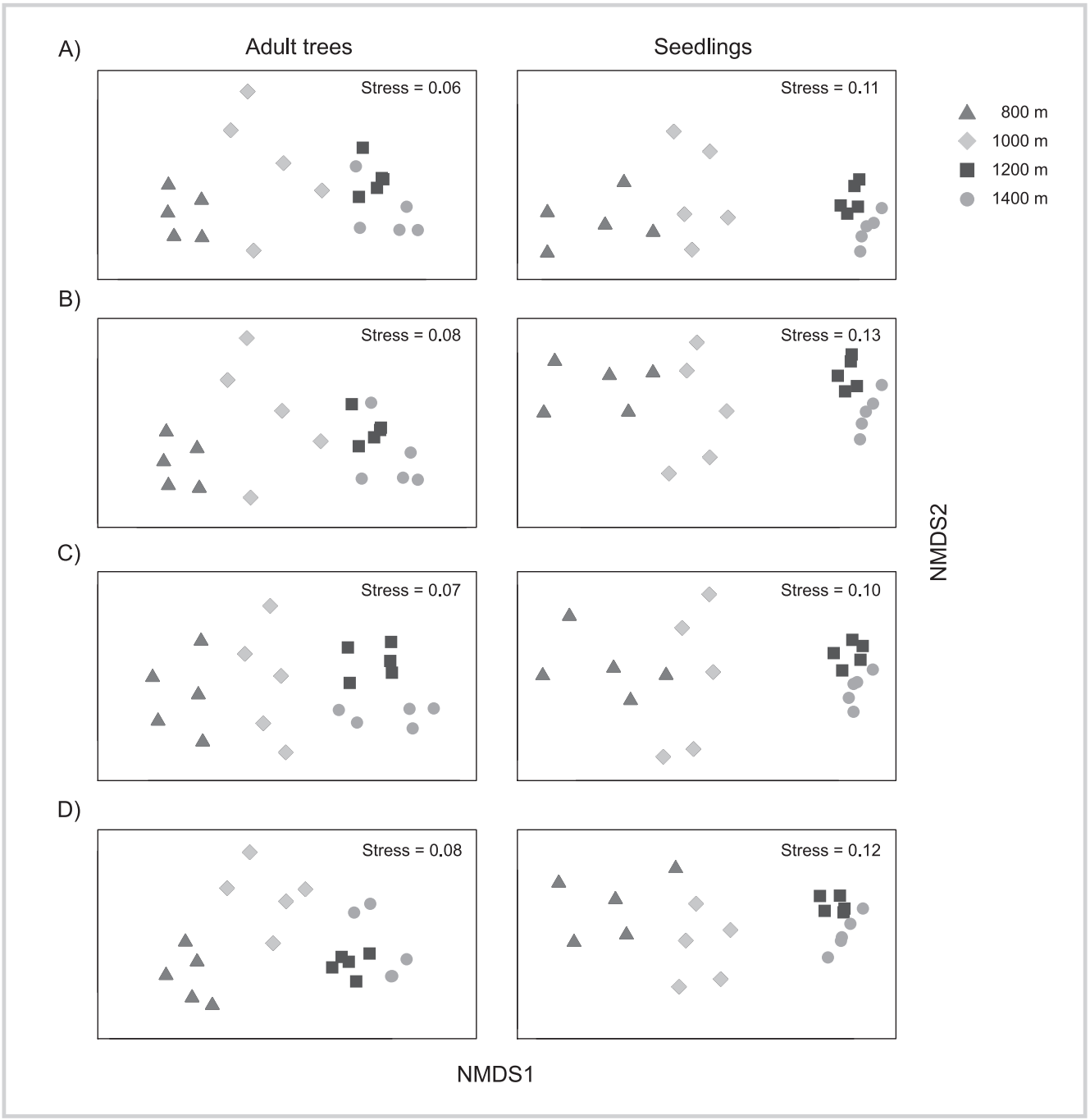
Diversity and species composition across elevations

Individual-based rarefaction curves showed greater observed and estimated (by extrapolation) species richness at lower (800 and 1000 m) than higher (1200 and 1400 m) elevational bands for both adult trees and seedlings (Figure 3). Within each of the lower and higher elevational bands, the differences in species richness were indistinguishable, with overlapping 95% confidence intervals. This was also statistically confirmed, with the results of ANOVA showing both adult trees and seedlings having higher species richness within lower elevational bands ($F = 67.56$ for adult trees, $F = 39.77$ for seedlings; see also Figure 4).

Regardless of the similarity indices used, NMDS ordinations showed clear elevational stratification in both adult tree and seedling species composition (Figure 3). PERMANOVA confirmed significant elevational differences ($P < 0.001$) for both adult tree and seedling

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FIGURE 3 Nonmetric multidimensional scaling ordinations in the 4 elevational bands based on different similarity indices: (A) Bray-Curtis; (B) Chao; (C) Jaccard; (D) Raup-Crick.



species composition. All of the ordinations showed a notable gap between the low elevations (800 and 1000 m) and the high elevations (1200 and 1400 m), and the sample dispersion was generally greater at the low elevations.

Temperature and soil moisture

Mean monthly temperature showed little difference in May–August among the elevational bands (Figure 2). Although the temperature was highly variable in September–December, it was generally warmer in the lower elevational bands. In contrast, temperatures in January–April were cooler at 800 m than at other elevational bands.

We found significant differences in soil moisture among the elevational bands in both wet and dry seasons ($F = 7.109$ and $F = 13.88$ in wet and dry seasons,

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FIGURE 4 Mean species richness of seedlings and adult trees in each elevational band. Lowercase letters indicate differences between elevational zones. Bars indicate standard errors.

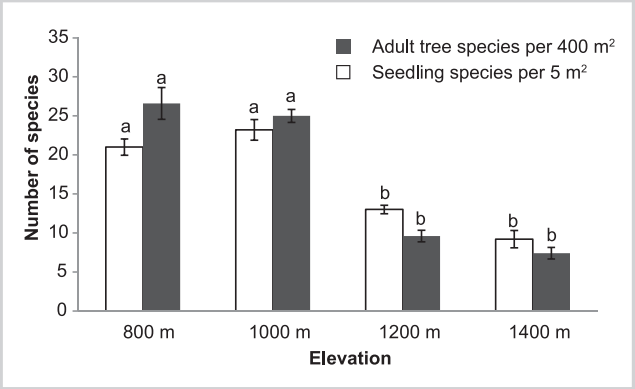
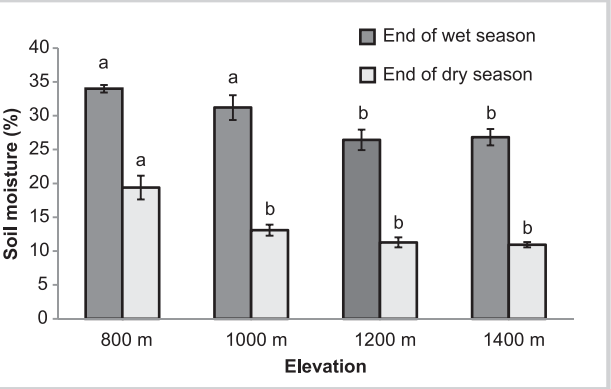


FIGURE 5 Soil moisture at 4 elevations at the end of the wet and dry seasons. Lowercase letters indicate differences in soil moisture. Bars indicate standard errors.



respectively). Post hoc tests showed that the wet season soil moisture was significantly greater at lower (800 and 1000 m) elevational bands (Figure 5). This pattern is consistent with those of adult and seedling species richness (Figure 4) and assemblage composition (Figure 3). In the dry season, only the soil moisture at 800 m was significantly higher, and soil moisture at 1000 m was not different from that at 1200 and 1400 m.

Relationships with environmental factors

For both partial (17 plots with 12 predictors) and full (20 plots with 8 predictors) datasets, the results of the information-theoretic approach suggested a number of plausible predictors that may explain the assemblage composition of adult and seedling species. Due to the spatially aggregated nature of the elevational transect, the spatial predictor (PCNM1) was plausible for both adult trees and seedlings (Tables 1 and 2). Elevation was also a plausible predictor for both adult trees and seedlings, with the exception of adult trees when using the full dataset (20 plots). No environmental predictors were selected for seedling assemblage composition, whereas mean temperature and dry season soil moisture were significantly associated with adult trees when using partial and full datasets, respectively.

Elevational distribution of adult trees and seedlings

We found 20 and 16 significant indicator species for adult trees and seedlings, respectively (Table 3). Of these, 19 were indicative of only 1 elevation (10 and 12 for adult trees and seedlings, respectively), 15 were indicative of 2 elevations (10 and 5 for adult trees and seedlings, respectively), and none was indicative of 3 or 4 elevations. All indicator species were restricted to either low (800 and 1000 m) or high (1200 and 1400 m) elevations. The only exception was *Aporosa yunnanensis*, whose adult trees and seedlings indicated elevations of 1000 and 1200 m. When both the adult trees and the seedlings of the same species were found to be indicators, their indicated elevations generally matched, with the exception of *C. echinocarpa*, whose seedlings showed a narrower elevational range than the adult trees.

Discussion

Diversity and species composition across elevations

We found a marked decrease in species richness from 1000 to 1200 m for both the adult tree and the seedling assemblages (Figure 4 and Table 4). Such a step-wise change in diversity patterns was also reported from other tropical mountains in Malesia (Van Steenis 1984), Borneo (Aiba and Kitayama 1999), Bolivia (Kessler 2000), Tanzania (Hemp 2006), and the Caribbean (Martin et al 2011).

Furthermore, we found a clear division in assemblage composition between low (800 and 1000 m) and high (1200 and 1400 m) elevations (Figure 3). This division was also evident in the indicator species, where only 1 species (*A. yunnanensis*) was indicative of both low and high elevational bands. Our results were consistent with previous research showing that large members of tropical tree species were restricted to a single forest type (Pitman et al 1999). The dominant tree species at low and high elevations belong to the genera *Parashorea* and *Castanopsis*, respectively (Table 3). These findings were consistent with previous studies based on adult trees (Wu et al 1987; Ohsawa 1993; Zhu et al 2006). The relative narrowness of the elevational distributions of dominant tree species is caused by opposing environmental constraints (Williams et al 2010; Arellano and Macía 2014). The vegetation changes observed in our study were likely influenced by strong seasonal dryness (and perhaps temperature—discussed later), with tropical rain forest occurring in wet valleys and tropical montane evergreen broad-leaved forest occurring in dry montane habitats (Zhu et al 2005).

Species composition was more similar for both adult trees and seedlings at high elevations (Figure 3). This may have resulted from drier environmental conditions at high elevations acting as an environmental filter and reducing species richness (Zhu et al 2005; Cao et al 2006). Aggregation of high-elevation plots was observed in NMDS ordinations of all 4 similarity indices, including the

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TABLE 1 Results of the information-theoretic analysis of assemblage composition of adult trees using 17 plots with all predictor variables.

Variable	Adult trees		Seedlings	
	Summed Akaike weights[a)]	*P*-value[b)]	Summed Akaike weights	*P*-value[b)]
Mean air temperature	3.810	**0.013**	0.931	0.118
Maximum air temperature	1.006	0.113	0.741	0.160
Minimum air temperature	0.594	0.134	0.659	0.159
Coefficient of variation of air temperatures	0.221	0.217	0.456	0.211
Elevation	3.059	**0.018**	7.561	**0.001**
Soil moisture in wet season	−0.645	0.799	−0.326	0.556
Soil moisture in dry season	1.209	0.102	−0.203	0.477
Seasonal variation of soil moisture	0.284	0.214	−0.717	0.822
Aspect	−0.661	0.890	−0.807	0.992
Slope	−0.462	0.658	−0.540	0.741
PCNM1[c)]	9.787	<**0.001**	5.363	**0.004**
PCNM2[c)]	−0.527	0.948	−0.631	0.999

[a)] Summed Akaike weights use the model averaging approach.
[b)] Significant *P* values are shown in bold.
[c)] PCNM1 and PCNM2 are the primary and secondary vectors of the principal coordinates of neighbor matrices.

Raup Crick index (a probabilistic measure unaffected by the number of species— Chase et al 2011), suggesting that the high similarity of these plots is not a simple artifact caused by depauperate flora at these elevations.

Associations with environmental factors

Elevation is a suitable proxy for varying environmental factors, as the assemblage composition of organisms and environmental characteristics generally change with

TABLE 2 Results of the information-theoretic analysis of assemblage composition of adult trees using all 20 plots without temperature predictors.

Variable	Adult trees		Seedlings	
	Summed Akaike weights[a)]	*P*-value[b)]	Summed Akaike weights	*P*-value[b)]
Elevation	−0.049	0.318	3.438	**0.016**
Soil moisture in wet season	0.280	0.215	−0.432	0.548
Soil moisture in dry season	2.949	**0.033**	−0.468	0.534
Seasonal variation of soil moisture	0.536	0.179	−0.550	0.639
Aspect	−0.656	0.935	−0.673	0.986
Slope	−0.634	0.817	−0.665	0.892
PCNM1[c)]	7.305	**0.000**	4.445	**0.011**
PCNM2[c)]	−0.651	0.985	−0.772	0.998

[a)] Summed Akaike weights use the model averaging approach
[b)] Significant *P* values are shown in bold.
[c)] PCNM1 and PCNM2 are the primary and secondary vectors of the principal coordinates of neighbor matrices.

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TABLE 3 Elevation-restricted species with significant indicator values of 60% or higher.[a)] (Table continued on next page.)

Species	Specimen type	Indicator value	Elevation indicated	Elevation at which species is present			
				800 m	1000 m	1200 m	1400 m
Trigonostemon thyrsoideus	Adult	60%	800 m	0.05			
	Seedling	*	*	0.01			
Artabotrys honkongensis	Adult	–	–				
	Seedling	**60%**	**800 m**	0.04			
Diospyros hasseltii	Adult	**60%**	**800 m**	0.05			
	Seedling	**60%**	**800 m**	0.04			
Diospyros nigrocortex	Adult	*	*	0.03			
	Seedling	**60%**	**800 m**	0.12			
Pometia tomentosa	Adult	**80%**	**800 m**	0.13			
	Seedling	**60%**	**800 m**	0.05			
Pseuduvaria indochinensis	Adult	*	*	0.01			
	Seedling	**100%**	**800 m**	0.11			
Parashorea chinensis	Adult	**87%**	**800 m**	0.50	0.03		
	Seedling	**63%**	**800 m**	0.14	0.04		
Antidesma montanum	Adult	**60%**	**800 m**	0.03			
	Seedling	*	*		0.01		
Nephelium chryseum	Adult	**80%**	**800 m, 1000 m**	0.04	0.11		
	Seedling	*	*		0.02		
Pittosporopsis kerrii	Adult	**80%**	**800 m, 1000 m**	0.22	0.12		
	Seedling	**90%**	**800 m, 1000 m**	0.30	0.10		
Baccaurea ramiflora	Adult	**80%**	**800 m, 1000 m**	0.09	0.08		
	Seedling	*	*	0.04			
Dichapetalum gelonioides	Adult	*	*	0.03			
	Seedling	**80%**	**800 m, 1000 m**	0.12	0.05		
Knema furfuracea	Adult	**70%**	**800 m, 1000 m**	0.04	0.10		
	Seedling	*	*		0.08		
Garcinia cowa	Adult	**70%**	**800 m, 1000 m**	0.08	0.10		
	Seedling	*	*	0.02	0.02	0.01	0.02
Litsea atrata	Adult	–	–				
	Seedling	**60%**	**1000 m**		0.03		
Tabernaemontana corymbosa	Adult	–	–				
	Seedling	**64%**	**1000 m**		0.04		0.02
Syzygium cumini	Adult	**80%**	**1000 m**		0.07		
	Seedling	–	–				

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TABLE 3 Continued. (First part of Table 3 on previous page.)

Species	Specimen type	Indicator value	Elevation indicated	Elevation at which species is present			
				800 m	1000 m	1200 m	1400 m
Alseodaphne petiolaris	Adult	**60%**	**1000 m**		0.21		
	Seedling	*	*	0.02	0.02		
Actinodaphne henryi	Adult	**60%**	**1000 m**		0.11		
	Seedling	*	*		0.03	0.01	
Aporosa yunnanensis	Adult	**90%**	**1000 m, 1200 m**		0.18	0.37	
	Seedling	**80%**	**1000 m, 1200 m**		0.06	0.14	
Castanopsis calathiformis	Adult	*	*				0.05
	Seedling	**81%**	**1200 m, 1400 m**		0.05	0.12	0.43
Castanopsis echinocarpa	Adult	**90%**	**1200 m, 1400 m**			0.53	0.33
	Seedling	**64%**	**1200 m**		0.20	0.81	0.09
Castanopsis mekongensis	Adult	**78%**	**1200 m, 1400 m**		0.10	0.43	0.91
	Seedling	*	*				0.03
Olea europaea	Adult	**–**	**–**				
	Seedling	**80%**	**1200 m**			0.07	
Schima wallichii	Adult	**–**	–				
	Seedling	**80%**	**1200 m**			0.06	
Wendlandia tinctoria	Adult	**69%**	**1200 m**			0.20	0.04
	Seedling	*	*			0.01	
Olea rosea	Adult	**60%**	**1200 m**			0.10	
	Seedling	*	*			0.02	
Lindera metcalfiana* var. *dictyophylla	Adult	–	–	0.01	0.03	0.07	0.12
	Seedling	**84%**	**1200 m, 1400 m**		0.01	0.31	0.34
Lithocarpus truncatus	Adult	**100%**	**1200 m, 1400 m**			0.47	0.60
	Seedling	–	–				
Schima argentea	Adult	**100%**	**1200 m, 1400 m**			0.36	0.35
	Seedling	–	–				
Vernonia solanifolia	Adult	–	–				
	Seedling	**60%**	**1400 m**				0.07

[a] * Indicates that the adult tree or seedling was not a significant indicator of any elevational band; – indicates that the adult tree or seedling was not present at any elevational band.

elevation in a progressive manner (with some exceptions—eg Salas-Morales and Meave 2012). Both adult tree and seedling compositions in our study, however, showed a clear division between high and low elevations, suggesting that some important environmental factors might change significantly across these elevations.

For adult trees, we found that mean temperature and dry-season soil moisture were plausible predictors, significantly associated with assemblage composition. Temperature, generally speaking, decreases linearly with elevation (Barry 1992). Our results, however, showed much lower mean temperature at 800 m (17.5 ± 0.34SE)

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TABLE 4 Species diversity indices for adult trees and seedlings at different elevations. Lowercase letters indicate significant differences between elevation zones.

Index	Specimen type	800 m	1000 m	1200 m	1400 m
Shannon-Wiener	Adult trees	3.111 ± 0.206a	3.075 ± 0.12a	2.132 ± 0.166b	1.873 ± 0.196b
	Seedlings	2.902 ± 0.087a	2.985 ± 0.112a	2.327 ± 0.11b	2.010 ± 0.358b
Simpson	Adult trees	0.946 ± 0.014ab	0.946 ± 0.01a	0.871 ± 0.022bc	0.832 ± 0.029c
	Seedlings	0.937 ± 0.003ab	0.941 ± 0.006ab	0.879 ± 0.015c	0.836 ± 0.069bc
Pielou	Adult trees	0.951 ± 0.017a	0.956 ± 0.015a	0.949 ± 0.009a	0.946 ± 0.027a
	Seedlings	0.955 ± 0.012ab	0.951 ± 0.008ab	0.908 ± 0.013c	0.918 ± 0.034bc

than at higher elevations (20.0 ± 0.02, 19.4 ± 0.18, and 18.4 ± 0.07 at 1000, 1200, and 1400 m, respectively) in the dry season (Figure 2). Several of the previous surveys in this area reported similar patterns in temperature (Guo and Zhong 1986; Zhong and Guo 1997). As the 800 m plots were all located within a mountain valley, our results may be attributable to cool air draining down into the valley and lifting the warm air to higher elevations (Miller et al 1983; Goulden et al 2006).

However, our results have caveats because the analysis included partial data (n = 17), which excluded 3 of the 1000 m plots due to loss of the thermo-loggers. Using the full 20 plots, we found that soil moisture in the dry season was a plausible environmental factor (Table 2). Soil moisture was significantly higher at 800 m than at other elevational bands at the end of the dry season, perhaps due to the presence of heavy fog in the lower valley (Cao et al 2006). Although similar results were found during the wet season, where soil moistures at both 800 and 1000 m were significantly higher than at 1200 and 1400 m, wet season soil moisture was not selected as plausible. This implies that limited soil moisture availability during the dry season may shape the elevational distribution of adult trees in this area. Water shortage has been associated with the distribution of tree species in many parts of the world. For example, in tropical montane forest, gullies and high elevations with light water stress are dominated by humid-condition species, while low elevations are dominated by dry-condition species (Ledo et al 2009). In subtropical forest, soil moisture drives change in elevational vegetation types (You et al 2013). This could even be aggravated in mountains dominated by monsoon climate. In the temperate forest, drought resistance ability significantly influenced the elevational positions of 5 pine species (Barton and Teeri 1993). In Panama, soil water availability was considered to be the main factor controlling the distribution of tropical tree species (Bunker and Carson 2005; Engelbrecht et al 2007), perhaps because the survival and growth of seedlings is constrained by the severity of drought in the dry season (Engelbrecht et al 2005; Slot and Poorter 2007; Comita and Engelbrecht 2009). Our study suggested that moisture availability and temperature regime, which are caused by the change of elevation, may determine the elevational distribution pattern of adult tree species.

We found that seedling composition, in contrast to that of adult trees, was only associated with elevation and spatial arrangement. Soil moisture and temperature were not selected as plausible predictors of seedling composition (Tables 1 and 2). The lack of plausible environmental predictors for seedling assemblage composition may suggest that environmental filtering only operates while trees are maturing (Grubb 1977; Poorter et al 2008). Our result suggests that the seedlings of high-elevation tree species established at low elevations may play an important role in shifting species ranges to stay in a suitable environmental envelope.

Elevational distributions of adult trees versus seedlings

We observed very similar elevational distributions for adult trees and seedlings of most indicator species (Table 3). Zhu et al (2014) also reported that most tree species in North America are not yet migrating in response to climate change. In our study, we found several tree species that dominate the evergreen broad-leaved forest at 1200 and 1400 m, such as *C. echinocarpa* and *C. calathiformis,* occurring at lower elevations where the tropical rain forest is distributed. However, we did not observe seedlings of tree species dominant at 800 m and 1000 m distributed in higher elevations. Under potential climate change regimes, these changes in the elevational distribution of seedlings may expand the range of tree species in the future and ultimately alter forest structure and processes. This suggests that the species currently dominant at high elevations might expand their range downward if future climate change causes habitats at lower elevations to become more suitable for their establishment (eg dryer). However, under the same climate change scenarios, species currently dominant at low elevations are unlikely to expand upslope because their seedlings are less adapted for the dryer habitats found at high elevations.

In a climate warming scenario, shifts in distribution range of seedlings may lead to shifts in the distribution range of tree species, which ultimately influences the structure and dynamics of the forest (Lenoir et al 2009;

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Rehm and Feeley 2013). Previous studies indicated that some species in temperate areas shifted their distribution to higher elevations because of climate warming (Wilson et al 2005; Lenoir et al 2008). In some tropical forests, climate warming is considered to be the main factor driving tree species to migrate upslope (Feeley et al 2013; Savage and Vellend 2015). However, such a situation may not take place in our study region, as the relatively dryer conditions at higher elevations may limit the uphill shift of tree species in tropical rain forests. Our results suggest that, as this region is predicted to become drier and hotter with climate change (He and Zhang 2005), the tropical rain forests at lower elevations may contract their distribution ranges as the habitats at lower elevations become drier, and species at higher elevations may shift their distributions downward.

Habitat modification can also be an alternative mechanism causing downslope range shifts (Lenoir et al 2010). A study in California suggested that species shift downhill in response to regional changes in climatic water balance (Crimmins et al 2011). Furthermore, our research region may face a significant loss of species diversity if tree species cannot shift their elevational distributions as quickly as climate change occurs (Corlett and Westcott 2013). Some tree species of the Fagaceae family may expand their local distribution. High-elevation species such as *C. echinocarpa* and *C. calathiformis* could likely shift to low-elevation areas, but the representative tree species of low-elevation tropical rain forests, such as *P. chinensis* and *Baccaurea ramiflora*, may narrow their distribution range. Under climate change regimes, this downhill migration of high-elevation species might also occur in other tropical and subtropical montane forests dominated by monsoon climate.

Conclusion

A step-wise decline in diversity was observed in this tropical montane forest. Our study also observed that a large number of tropical tree species are restricted to a narrow elevational range, and environmental filtering regulates species distribution while trees are maturing. Furthermore, we found a trend in which the seedlings of high-elevation species migrate downhill, suggesting that local climate change might result in the contraction of tropical rain forest at lower elevations and the expansion of higher tropical montane tree species downhill. Long-term monitoring of seedling dynamics and a transplant experiment would help us to predict potential changes in tree species distribution under climate change regimes, and this is strongly recommended for future research.

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REFERENCES

Aiba S, Kitayama K. 1999. Structure, composition and species diversity in an altitude–substrate matrix of rain forest tree communities on Mount Kinabalu, Borneo. *Plant Ecology* 140:139–157.

Anderson MJ. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26:32–46.

Angelo CL, Daehler CC. 2013. Upward expansion of fire-adapted grasses along a warming tropical elevation gradient. *Ecography* 36:551–559.

Anthelme F, Dangles O. 2012. Plant–plant interactions in tropical alpine environments. *Perspectives in Plant Ecology Evolution and Systematics* 14:363–372.

Arellano G, Macía MJ. 2014. Local and regional dominance of woody plants along an elevational gradient in a tropical montane forest of northwestern Bolivia. *Plant Ecology* 215:39–54.

Bace R, Svoboda M, Pouska V, Janda P, Cervenka J. 2012. Natural regeneration in Central-European subalpine spruce forests: Which logs are suitable for seedling recruitment? *Forest Ecology and Management* 266:254–262.

Bansal S, Germino J. 2010. Variation in ecophysiological properties among conifers at an ecotonal boundary: Comparison of establishing seedlings and established adults at timberline. *Journal of Vegetation Science* 21:133–142.

Barry RG. 1992. *Mountain Weather and Climate*. New York, NY: Routledge.

Barton AM, Teeri JA. 1993. The ecology of elevational positions in plants: Drought resistance in five montane pine species in southeastern Arizona. *American Journal of Botany* 80:15–25.

Bohlman SA, Laurance WF, Laurance SG, Nascimento HEM, Fearnside PM, Andrade A. 2008. Importance of soils, topography and geographic distance in structuring central Amazonian tree communities. *Journal of Vegetation Science* 19:863–874.

Buckley LB, Jetz W. 2008. Linking global turnover of species and environments. *Proceedings of the National Academy of Sciences of the United States of America* 105:17836–17841.

Bunker DE, Carson WP. 2005. Drought stress and tropical forest woody seedlings: Effect on community structure and composition. *Journal of Ecology* 93:794–806.

Burnham KP, Anderson DR. 2002. *Model Selection and Multi-model Inference: A Practical Information-Theoretic Approach*. New York, NY: Springer.

Cao M, Zhang J. 1997. Tree species diversity of tropical forest vegetation in Xishuangbanna, SW China. *Biodiversity and Conservation* 6:995–1006.

Cao M, Zou X, Warren M, Zhu H. 2006. Tropical forests of Xishuangbanna, China. *Biotropica* 38:306–309.

Chao A, Chazdon RL, Colwell RK, Shen TJ. 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters* 8:148–159.

Chase JM, Kraft NJB, Smith KG, Vellend M, Inouye BD. 2011. Using null models to disentangle variation in community dissimilarity from variation in alpha-diversity. *Ecosphere* 2:art24.

Chen IC, Hill JK, Ohlemuller R, Roy DB, Thomas CD. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333:1024–1026.

Comita LS, Engelbrecht BMJ. 2009. Seasonal and spatial variation in water availability drive habitat associations in a tropical forest. *Ecology* 90:2755–2765.

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Corlett RT, Westcott DA. 2013. Will plant movements keep up with climate change? *Trends of Ecology and Evolution* 28:482–488.
Crimmins SM, Dobrowski SZ, Greenberg JA, Abatzoglou JT, Mynsberge AR. 2011. Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science* 331:324–327.
Curtis JT, McIntosh RP. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology* 32:476–496.
Dray S, Legendre P, Peres-Neto PR. 2006. Spatial modelling: A comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling* 196:483–493.
Dufrêne M, Legendre P. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs* 67:345–366.
Engelbrecht BMJ, Comita LS, Condit R, Kursar TA, Tyree MT, Turner BL, Hubbell SP. 2007. Drought sensitivity shapes species distribution patterns in tropical forests. *Nature* 447:80–82.
Engelbrecht BMJ, Kursar TA, Tyree MT. 2005. Drought effects on seedling survival in a tropical moist forest. *Trees* 19:312–321.
Feeley KJ, Hurtado J, Saatchi S, Silman MR, Clark DB. 2013. Compositional shifts in Costa Rican forests due to climate-driven species migrations. *Global Change Biology* 19:3472–3480.
Feeley KJ, Silman MR, Bush MB, Farfan W, Cabrera KG, Malhi Y, Meir P, Revilla NS, Quisiyupanqui MNR, Saatchi S. 2011. Upslope migration of Andean trees. *Journal of Biogeography* 38:783–791.
Goulden ML, Miller SD, da Rocha HR. 2006. Nocturnal cold air drainage and pooling in a tropical forest. *Journal of Geophysical Research* 111:D8.
Grubb PJ. 1977. Maintenance of species-richness in plant communities—Importance of regeneration niche. *Biological Reviews of the Cambridge Philosophical Society* 52:107–145.
Grytnes JA, McCain CM. 2007. Elevational trends in biodiversity. *In:* Levin S, editor. *Encyclopaedia of Biodiversity*. New York, NY: Elsevier Science Publishers, pp 1–8.
Guo Y, Zhong S. 1986. The mountain temperature inversion in Xishuangbanna of Yunnan [in Chinese with English abstract]. *Tropical Geography* 6:18–22.
He YL, Zhang YP. 2005. Climate change from 1960–2000 in the Lancang River Valley, China. *Mountain Research and Development* 25:341–348.
Hemp A. 2006. Continuum or zonation? Altitudinal gradients in the forest vegetation of Mt. Kilimanjaro. *Plant Ecology* 184:27–42.
Hillyer R, Silman MR. 2010. Changes in species interactions across a 2.5 km elevation gradient: Effects on plant migration in response to climate change. *Global Change Biology* 16:3205–3214.
Itow S. 1991. Species turnover and diversity patterns along an evergreen broad-leaved forest coenocline. *Journal of Vegetation Science* 2:477–484.
Jones MM, Szyska B, Kessler M. 2011. Microhabitat partitioning promotes plant diversity in a tropical montane forest. *Global Ecology and Biogeography* 20:558–569.
Kessler M. 2000. Elevational gradients in species richness and endemism of selected plant groups in the central Bolivian Andes. *Plant Ecology* 149:181–193.
Körner C. 2007. The use of "altitude" in ecological research. *Trends of Ecology and Evolution* 22:569–574.
Ledo A, Montes F, Condes S. 2009. Species dynamics in a montane cloud forest: Identifying factors involved in changes in tree diversity and functional characteristics. *Forest Ecology and Management* 258:S75–S84.
Legendre P, Legendre LF. 2012. *Numerical Ecology*. Amsterdam, Netherlands: Elsevier.
Lenoir J, Gégout JC, Guisan A, Vittoz P, Wohlgemuth T, Zimmermann NE, Dullinger S, Pauli H, Willner W, Svenning J-C. 2010. Going against the flow: Potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography* 33:295–303.
Lenoir J, Gégout JC, Marquet P, De Ruffray P, Brisse H. 2008. A significant upward shift in plant species optimum elevation during the 20th century. *Science* 320:1768–1771.
Lenoir J, Gégout JC, Pierrat JC, Bontemps JD, Dhote JF. 2009. Differences between tree species seedling and adult altitudinal distribution in mountain forests during the recent warm period (1986–2006). *Ecography* 32:765–777.
Leuschner C. 2000. Are high elevations in tropical mountains arid environments for plants? *Ecology* 81:1425–1436.
Li XS, Liu WY, Tang CQ. 2010. The role of the soil seed and seedling bank in the regeneration of diverse plant communities in the subtropical Ailao Mountains, Southwest China. *Ecological Research* 25:1171–1182.
Lomolino M. 2001. Elevation gradients of species-density: Historical and prospective views. *Global Ecology and Biogeography* 10:3–13.
Magurran AE. 1988. *Ecological Diversity and Its Measurement*. Dordrecht, Netherlands: Springer.
Marcora PI, Renison D, Pais-Bosch AI, Cabido MR, Tecco PA. 2013. The effect of altitude and grazing on seedling establishment of woody species in central Argentina. *Forest Ecology and Management* 291:300–307.
Martin PH, Fahey TJ, Sherman RE. 2011. Vegetation zonation in a neotropical montane forest: Environment, disturbance and ecotones. *Biotropica* 43:533–543.
McArdle BH, Anderson MJ. 2001. Fitting multivariate models to community data: A comment on distance-based redundancy analysis. *Ecology* 82:290–297.
Meier ES, Lischke H, Schmatz DR, Zimmermann NE. 2012. Climate, competition and connectivity affect future migration and ranges of European trees. *Global Ecology and Biogeography* 21:164–178.
Miller DR, Bergen JD, Neuroth G. 1983. Cold air drainage in a narrow forested valley. *Forest Science* 29:357–370.
Minchin PR. 1987. An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* 69:89–107.
Nakamura A, Burwell CJ, Lambkin CL, Katabuchi M, McDougall A, Raven RJ, Neldner VJ. 2015. The role of human disturbance in island biogeography of arthropods and plants: An information theoretic approach. *Journal of Biogeography* 42:1406–1417.
Ohsawa M. 1993. Latitudinal pattern of mountain vegetation zonation in southern and eastern Asia. *Journal of Vegetation Science* 4:13–18.
Oliveira-Filho AT, Fontes MAL. 2000. Patterns of floristic differentiation among Atlantic forests in southeastern Brazil, and the influence of climate. *Biotropica* 32:793–810.
Parolo G, Rossi G. 2008. Upward migration of vascular plants following a climate warming trend in the Alps. *Basic and Applied Ecology* 9:100–107.
Patten RS, Ellis JE. 1995. Patterns of species and community distributions related to environmental gradients in an arid tropical ecosystem. *Vegetatio* 117:69–79.
Pereira JAA, Oliveira-Filho AT, Lemos-Filho JP. 2007. Environmental heterogeneity and disturbance by humans control much of the tree species diversity of Atlantic montane forest fragments in SE Brazil. *Biodiversity and Conservation* 16:1761–1784.
Pitman NCA, Terborgh J, Silman MR, Nuñez P. 1999. Tree species distributions in an upper Amazonian forest. *Ecology* 80:2651–2661.
Poorter L, Wright SJ, Paz H, Ackerly DD, Condit R, Ibarra-Manriques G. 2008. Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. *Ecology* 89:1908–1920.
Rehm EM, Feeley KJ. 2013. Forest patches and the upward migration of timberline in the southern Peruvian Andes. *Forest Ecology and Management* 305:204–211.
Ross RIC, Agren JA, Pannell JR. 2012. Exogenous selection shapes germination behaviour and seedling traits of populations at different altitudes in a Senecio hybrid zone. *Annuals of Botany* 110:1439–1447.
Salas-Morales SH, Meave JA. 2012. Elevational patterns in the vascular flora of a highly diverse region in southern Mexico. *Plant Ecology* 213:1209–1220.
Sanchez M, Pedroni F, Eisenlohr PV, Oliveira-Filho AT. 2013. Changes in tree community composition and structure of Atlantic rain forest on a slope of the Serra do Mar range, Southeastern Brazil, from near sea level to 1000 m of altitude. *Flora* 208:184–196.
Savage J, Vellend M. 2015. Elevational shifts, biotic homogenization and time lags in vegetation change during 40 years of climate warming. *Ecography* 38:546–555.
Slot M, Poorter L. 2007. Diversity of tropical tree seedling responses to drought. *Biotropica* 39:683–690.
Teketay D. 1997. Seedling populations and regeneration of woody species in dry Afromontane forests of Ethiopia. *Forest Ecology and Management* 98:149–165.
Urbieta IR, García LV, Zavala MA, Marañón T. 2011. Mediterranean pine and oak distribution in southern Spain: Is there a mismatch between regeneration and adult distribution? *Journal of Vegetation Science* 22:18–31.
Van Steenis CGGJ. 1984. Floristic altitudinal zones in Malesia. *Botanical Journal of the Linnean Society* 89:289–292.
Vazquez JA, Givnish TJ. 1998. Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlan. *Journal of Ecology* 86:999–1020.
Vera ML. 1997. Effects of altitude and seed size on germination and seedling survival of heathland plants in North Spain. *Plant Ecology* 133:101–106.
Vitasse Y, Hoch G, Randin CF, Lenz A, Kollas C, Körner C. 2012. Tree recruitment of European tree species at their current upper elevational limits in the Swiss Alps. *Journal of Biogeography* 39:1439–1449.
Wang Y, Naumann U, Wright ST, Warton DI. 2012. Mvabund—An R package for model-based analysis of multivariate abundance data. *Methods in Ecology and Evolution* 3:471.
Whittaker RH. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30:279–338.
Williams JN, Viers JH, Schwartz MW. 2010. Tropical dry forest trees and the relationship between local abundance and geographic range. *Journal of Biogeography* 37:951–959.

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Wilson RJ, Gutierrez D, Gutierrez J, Martinez D, Agudo R, Monserrat VJ. 2005. Changes to the elevational limits and extent of species ranges associated with climate change. *Ecology Letters* 8:1138–1146.
Wolf JHD. 1993. Diversity patterns and biomass of epiphytic bryophytes and lichens along an altitudinal gradient in the northern Andes. *Annals of the Missouri Botanical Garden* 80:928–960.
Wu Z. 1980. *The Vegetation of China* [in Chinese]. Beijing, China: Scientific Press.
Wu Z, Zhu Y, Jiang H. 1987. *The Vegetation of Yunnan* [in Chinese]. Beijing, China: Scientific Press.
You G, Zhang Y, Liu Y, Schaefer D, Gong H, Gao J. 2013. Investigation of temperature and aridity at different elevations of Mt. Ailao, SW China. *International Journal of Biometeorology* 57:487–492.
Zhang J, Cao M. 1995. Tropical forest vegetation of Xishuangbanna, SW China and its secondary changes, with special reference to some problems in local nature conservation. *Biological Conservation* 73:229–238.
Zhong S, Guo Y. 1997. Study on inversion of mountains in Xishuangbanna [in Chinese with English abstract]. *Journal of Yunnan Tropical Crops Science, Technology* 20:4–11.
Zhu H, Cao M, Hu H. 2006. Geological history, flora, and vegetation of Xishuangbanna, southern Yunnan, China. *Biotropica* 38:310–317.
Zhu H, Shi J, Zhao C. 2005. Species composition, physiognomy and plant diversity of the tropical montane evergreen broad-leaved forest in southern Yunnan. *Biodiversity and Conservation* 14:2855–2870.
Zhu K, Woodall CW, Ghosh S, Gelfand AE, Clark JS. 2014. Dual impacts of climate change: Forest migration and turnover through life history. *Global Change Biology* 20:251–264.

Supplemental material

TABLE S1 Location of the 20 plots on the elevational transect.

TABLE S2 Importance values of adult tree species at each of the 4 elevational bands. Species with the highest importance values within each band are shown in bold.

TABLE S3 Importance values of tree seedling species at each of the 4 elevational bands. Species with the highest importance values within each band are shown in bold.

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