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Original Research Article

Tree species of tropical and temperate lineages in a tropical Asian montane forest show different range dynamics in response to climate change

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ABSTRACT

Shifts in species distributions have been documented in response to recent climatic change, with most species moving poleward and to higher altitude. However, different taxa may respond to climatic change differently. The Climatic Variability Hypothesis (CVH) suggests that taxa originating from environmentally variable habitats, such as those at high latitudes and altitudes, should evolve wider environmental tolerances and greater dispersal capacity, and consequently be less responsive to climatic change than taxa originating from relatively stable habitats. However, empirical tests of this hypothesis, especially in the Asian tropics, are scarce. In this study, we assessed the range dynamics of 20 tree species, by using the abundance and mean tree diameter and the ratio of juveniles to trees along an altitudinal transect (2450 m–3070 m) in a montane forest located in the southeastern Himalayas in Myanmar. We also compared the suitable range sizes of tree species of different range dynamics category. Among the species investigated, 12 experienced significant upward range extensions and other eight species experienced no-upward extensions. The modeled distribution range size of the 'upward species' were marginally significant narrower than those of 'non-upward' species. The 'upward' species were also often species of tropical evolutionary origin and the 'non-upward' species were of subtropics and temperate origin. The mechanism behind these distribution patterns of different species may be complex while the distribution patterns of this 20 species along the altitudinal transect generally support the prediction of the CVH. From the perspective of conserving biodiversity against the impacts of climatic change, more attention needs to be paid to narrowly distributed species, which are typically tropical origin, by enhancing connectivity and dispersal capacity in fragmented landscapes.

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1. Introduction

Anthropogenic climate change is fundamentally impacting on most ecological processes (Scheffers et al., 2016). Species range shifts and changes in vegetation composition and structure show particularly strong climate fingerprints (Kelly and Goulden, 2008; Costion et al., 2015; Peters et al., 2019). Accelerated warming is leading to pronounced poleward and upward shifts in plant species' ranges, both in high latitude and high altitude areas (Kelly and Goulden, 2008; Morueta-Holme et al., 2015; Sittaro et al., 2017; Steinbauer et al., 2018) and in lowland regions (Colwell et al., 2008; Bertrand et al., 2011). While upslope range expansion of species is expected with continued warming, range dynamics of plant species along altitudinal gradients do not always follow a uniform pattern (Corlett and Westcott, 2013; Sittaro et al., 2017). Better understanding of how plant species shift their ranges in response to climatic change is a research priority for documenting the impacts and consequences of planetary change in the Anthropocene (Corlett, 2015; Steinbauer et al., 2018; Peters et al., 2019), particularly for hyper-diverse tropical forests.

Tropical mountains are among the global biodiversity hotspots with high endemism and are home to thousands of plant and animal species (Myers et al., 2000; Polato et al., 2018; Peters et al., 2019). The functioning of tropical montane ecosystems support essential services to human societies, including carbon storage, water supply, and many others (Colwell et al., 2008; Steinbauer et al., 2018). However, the effects of climatic change on tropical mountain ecosystems have not been well explored (Bush et al., 2004; Rehm, 2014). Among a few studies, Morueta-Holme et al. (2015) investigated vegetation shifts in the tropical Andes within the past 210 years, and showed that most species experienced upward range shifts. In the meantime, there is still debate about whether tropical species are synchronously tracking the global warming, as some are lagging behind the climate envelope (Bertrand et al., 2011; Corlett and Westcott, 2013; Sittaro et al., 2017). To our knowledge, although some studies have been conducted in the tropics of Africa and South America (Colwell et al., 2008; Morueta-Holme et al., 2015; Polato et al., 2018), there are no studies of effects of climate change on montane tree communities in tropical Asia.

Several hypotheses have been proposed predicting patterns in species distribution range shifts in response to climatic change (Stevens, 1989; Gaston et al., 1998; Pintor et al., 2015). Among these, the Climatic Variability Hypothesis (CVH) suggests that organisms from environmentally variable habitats, such as those at high latitudes and altitudes, should evolve broader environmental tolerances and greater dispersal capacity, and consequently may be less impacted by climatic change than organisms originating from relatively stable habitats (Janzen, 1967; Stevens, 1989). Under the scenario of CVH, due to higher climatic variability, species from higher latitudes have broader environmental tolerances than tropical species; this enables them to have larger geographic ranges (Janzen, 1967; Stevens, 1989; Gaston et al., 1998). Thus, present-day differences in range sizes and breadth of tolerances have been amplified by evolutionary responses to past climatic fluctuations (Dynesius and Jansson, 2000). Dispersal capacity also influences distribution and range shifts (Corlett, 2009, 2017; Rehm, 2014; Abedi-Lartey et al., 2016; Howe, 2016); obviously, without dispersal and successful recruitment, no range shifts will occur. Generally, species with greater dispersal capacity have wider distribution ranges (Dynesius and Jansson, 2000). Despite documentation of these general patterns, empirical tests of the predictive power of CVH across taxa and environments, e.g., by examining whether breadth of tolerance is correlated with size of the species' geographic range, and whether dispersal capacity differs between species of different evolutionary origins, are limited (Addo-Bediako et al., 2000; Dynesius and Jansson, 2000), particularly for tree species (Pintor et al., 2015; Polato et al., 2018).

In this study, we conducted surveys of forest plots along an altitudinal transect in Natma Taung National Park (NTNP), Myanmar, a mountainous area located in the southeastern Himalayas with altitude ranging from 740 m to 3074 m a.s.l. Flora of the study region comprises a mixture of species from tropical, subtropical and temperate origins. Species range shifts begin when smaller and younger individuals establish outside the places where adults already occurred. Disappearance of mature trees from parts of the current range that have become unfavorable also contributes to range shift, though this may be associated with a long time lag (Vetaas, 2002; Yang et al., 2018). Thus, here, we aimed to answer the following research questions: (1) Do tree species in this area show range shifts in response to climate change? (2) If so, are species with narrow geographic ranges more likely to show range shifts, as predicted by the CVH? (3) Do species belonging to lineages of tropical and temperate/subtropical origin differ in size of their geographic ranges and in their response to climate change, as predicted by the CVH?

2. Material and methods

2.1. Study area

The study was conducted in Natma Taung National Park (NTNP), Chin State, north-western Myanmar (21°13′ N, 93°53′ E) (Fig. 1). The NTNP covers an area of 713.5 km^2. It was accredited as a Heritage Park of the Association of Southeast Asian Nations in 2012 and falls under the International Union for Conservation of Nature (IUCN) management category II. It also stands as a major component of the Indo-Burma Biodiversity Hotspot Region (www.cepf.net), and was listed as one of the Alliance for Zero Extinction sites (http://zeroextinction.org/). The topography is characterized by steep and rugged mountains, with altitude ranging from 740 m to 3074 m above sea level (a.s.l.). Vegetation cover at low altitudes is dry dipterocarp forests, passing through oak forests to meadow grassland at the highest summit. This area has been protected as a Reserved Forest since 1936. Due to conservation efforts and difficulty of access, the montane forest areas in this region have experienced very little direct disturbances from human activities. Counting of tree-rings in cores of selected trees (*Rhododendron arboreum*) across all the study sites showed that the oldest trees are around 250 years old (247.5 ± 11.1, $n = 12$) in this montane forest (authors' unpublished data),

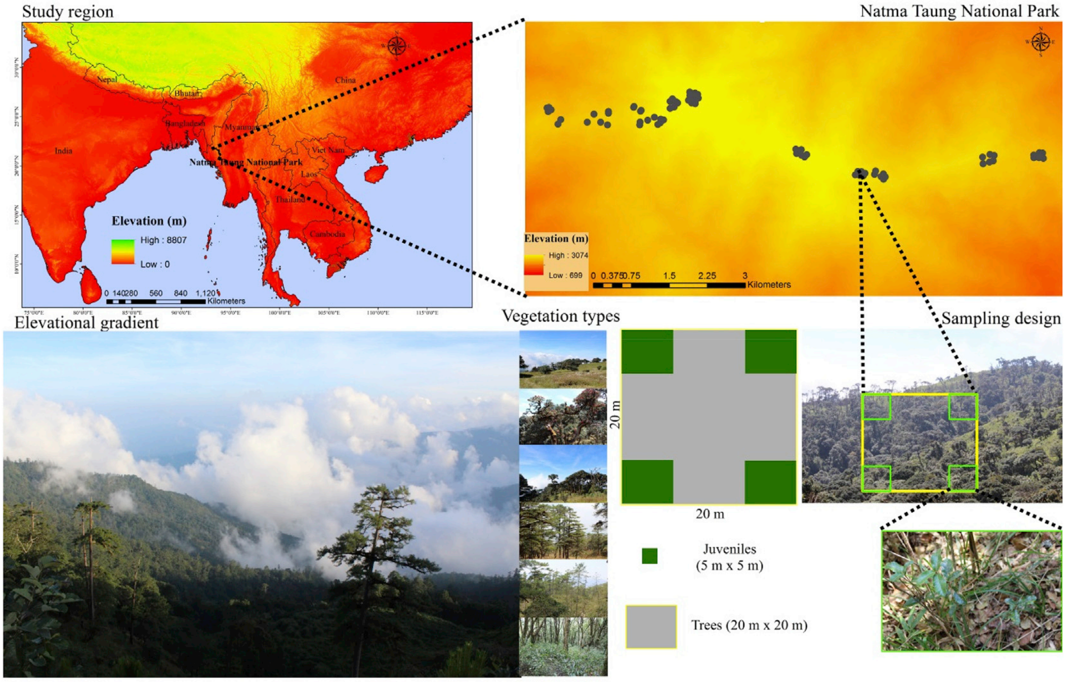

Fig. 1. Location of study area and sampling plots in Natma Taung National Park, Myanmar.

suggesting that forests in the study sites have experienced at least 250 years without clear-cutting or other massive human disturbances.

2.2. Climate and climatic data

The study area experiences a tropical monsoon climate. Weather records from the nearest meteorological station (16 km distant, at 1400 m a.s.l. in Mindat District) showed that in the period 1985–2017, mean annual temperature and precipitation were 20.5 °C and 1530 mm, respectively (Department of Hydrometeorology, Myanmar). There are three seasons in this region: winter (November to February), summer (March to mid-May) and the rainy (mid-May to October) season which is mainly driven by monsoon. As the local weather stations can provide data only for maximum 32 years, we used long-term climate data (1901–2017) from the Climate Research Unit database (CRU TS4.02, University of East Anglia, UK) as a surrogate. Comparing the data from the Climate Research Unit with the local weather station for the past 30 years, it showed a consistent trend with each other. Thus, we used these long-term climate data to assess the climate trend over the study region (Fig. 2a,b,c). We also downloaded 19 bioclimatic variables (Table A1) from the WorldClim database at 2.5 arc min resolution (Hijmans et al., 2005) and used them in calculating the suitable distribution range size of species.

2.3. Field sampling

Sampling was conducted along altitudinal transects extending from 2450 m to 3070 m a.s.l. Two transects were laid along altitudinal gradients and in each transect, six 20 m x 20 m plots were laid out within each 100 m altitudinal band. Thus, a total of 72 plots were created in the study site. Within each 20 m × 20 m plot, we nested four 5 m × 5 m plots, one in each corner (Fig. 1). Individual ≥10 cm diameter at breast height (DBH) were enumerated in each entire 20 m × 20 m plot and scored as mature trees; individual < 10 cm DBH were enumerated in the nested 5 m × 5 m plots and scored as juveniles. We also recorded geographic locations of all plots.

2.4. Measurements for estimation of range dynamics

Altogether 30 tree species were recorded along altitudinal transects. Ten species could not be included in analyses owing to the very small number of adult individuals (<25), or because they were found only within one altitudinal band. In assessing range dynamics over altitudinal gradients, we assumed that if a species is extending upslope, smaller individuals would be proportionally better represented at higher elevations than those of larger individuals. Unlike other, long-term empirical studies conducted on range shifts of species (e.g., Morueta-Holme et al., 2015), we conducted and analyzed data from a single time visit. Thus, we could not differentiate range shifts over consecutive years. We estimated range dynamics of species by using abundance data,

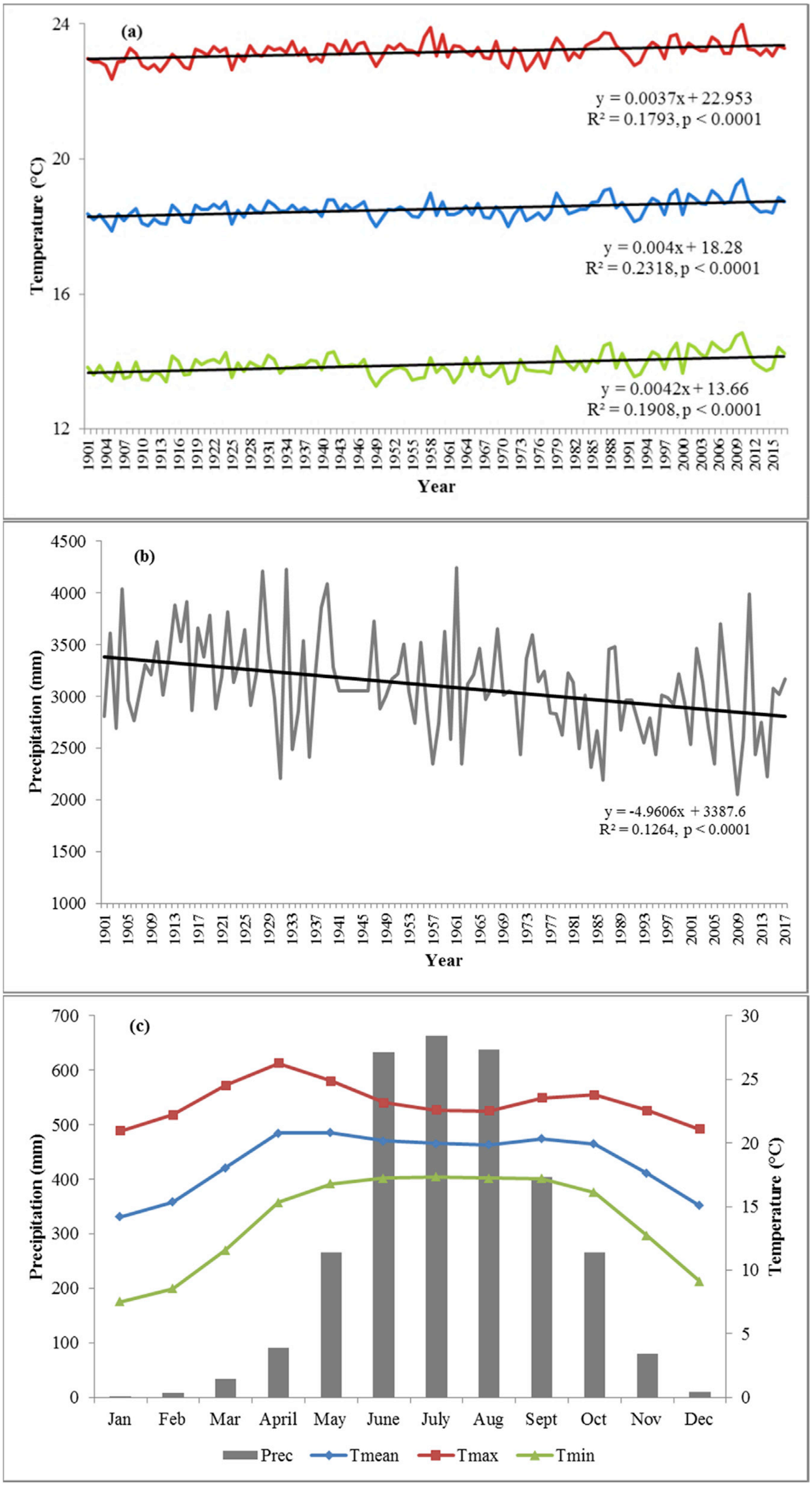

Fig. 2. Annual precipitation and temperatures from 1901 to 2017 over the study area, Natma Taung National Park, Myanmar. Red line = maximum temperature, blue line = mean temperature, green line = minimum temperature, grey line and bar = precipitation. **(a)** Mean annual temperatures**; (b)** mean annual precipitation and **(c)** mean monthly precipitation and temperatures. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Species-specific model parameters used in the final MaxEnt modeling analyses. Numbers of environmental variables used correspond to standard bioclimatic variables from WorldClim.

Species	Occurrence records	BioClim environmental variables used
Adinandra megaphylla	26	1,3,4,12,13,15,18
Betula alnoides	113	1,3,4,12,13,15,18
Castanopsis tribuloides	103	1,4,12,13,15,18
Cinnamomum tamala	66	1,3,4,12,13,15,18
Eriobotrya bengalensis	52	1,3,4,12,13,15,18
Lithocarpus magnificus	30	1,3,4,12,13,15,18
Lithocarpus wallichianus	28	1,3,4,12,13,15,18
Lithocarpus xylocarpus	37	4,13,15,18
Litsea monopetala	118	1, 12,13,18
Lyonia ovalifolia	772	1,3,4,12,13,15,18
Myrsine semiserrata	350	1,4, 12,18
Osmanthus yunnanensis	41	1,3,4,12
Pinus kesiya	60	4, 12,13,18
Quercus semecarpifolia	93	1,3,4,15
Rhododendron arboreum	68	1,3,4,12,13,18
Schefflera delavayi	168	1,3,4,12,13,15,18
Symplocos dryophila	140	1,3,4,13,15,18
Symplocos lucida	49	1,4,12,13,18
Viburnum cylindricum	244	1,3,4, 13,15,18
Viburnum erubescens	82	1,4,12,18

mean diameter of trees and proportion of juvenile to tree along altitudinal gradients. We assessed the range dynamics of tree species based on their diameter distribution and their geographic position along an altitudinal gradient, i.e., if smaller tree individuals (indicated by the average value of DBH) located in higher elevation bands than larger tree individuals, we categorized these as ‘upward’ species; similarly, if the DBH keep consistent along different altitudinal gradient, we categorized them as ‘non-upward’ species. In addition, in the upward scenario, the ratio of juvenile to trees would be high at the species’ upper altitudinal band. In the non-upward scenario, the ratio of juvenile to trees would be low at the species’ upper altitudinal band. The study method used here should under the assumption that smaller trees is indeed younger in age, which appears to be the case in our study site. Evidence for that was from the tree ring data for one species (*Rhododendron arboreum*) that we found positive correlations between DBH and age at all the six altitudinal bands while the altitude itself did not provide significant explanation to the DBH (Table A2). Furthermore, when we compared the age of same-sized trees (20 cm DBH class) at different altitudinal bands, there were no marked differences in ages of trees (20 cm—120 cm DBH) (authors’ unpublished data).

2.5. Estimation for species distribution range size

Maximum Entropy (MaxEnt ver. 3.4.1) species distribution modeling (Phillips et al., 2006) was used to estimate size of the geographic range of each of the 20 tree species analyzed. We used MaxEnt, a machine-learning method, as it is easier to use and has

Table 2
Range dynamics of species, estimated range size and dispersal syndrome.

Species and range dynamics	Estimated range size (km^2)	Dispersal syndrome
Upward		
Adinandra megaphylla	296805	Bats, rodents
Betula alnoides	667762	Birds, wind
Castanopsis tribuloides	360337	Birds, rodents, wind
Cinnamomum tamala	289588	Birds, rodents, wind
Eriobotrya bengalensis	961250	Bats, birds
Lithocarpus magnificus	689613	Rodents
Lithocarpus wallichianus	988730	Rodents
Rhododendron arboreum	340509	Birds, wind
Schefflera delavayi	127061	Bats, rodents
Symplocos dryophila	177917	Birds
Symplocos lucida	299479	Birds
Viburnum cylindricum	229433	Birds, rodents
Non-upward		
Lithocarpus xylocarpus	398448	Rodents
Litsea monopetala	1155184	Bats, birds
Lyonia ovalifolia	651647	Rodents, wind
Myrsine semiserrata	721117	Birds, rodents, wind
Osmanthus yunnanensis	696356	Birds, rodents
Quercus semecarpifolia	501185	Birds, rodents, wind
Pinus kesiya	875574	Bats, rodents
Viburnum erubescens	456544	Birds, rodents

been reported to have greater accuracy than other modeling methods in predicting species distributions (Merow et al., 2013, Costion et al., 2015; Qin et al., 2017). MaxEnt is widely used in species distribution modeling and in calculating species range sizes, and is also quite suitable for calibrating the data approximately to the existing habitats (Pearson et al., 2007; Costion et al., 2015). Furthermore, MaxEnt performs well even when the number of occurrence records is fewer than 25 (Pearson et al., 2007). We collected the species location data from the Global Biodiversity Information Facility (www.gbif.org), iDigBio (https://idigbio.org/), Harvard University Herbarium (https://kiki.huh.harvard.edu/databases/) and Flora Malesiana (http://portal.cybertaxonomy.org/flora-malesiana/node/9414). We then screened the downloaded data. Models were trained based on the occurrence points of each species, ranging from 26 to 772 (mean 132) points (Table 1). When the number of environmental variables used in the model is larger than the number of occurrence records, it could bias the results in training the model (Costion et al., 2015). However, in our study, numbers of occurrence records of each species were greater than the number of variables included in modeling. We used 19 bioclimatic variables downloaded from the WorldClim database (www.worldclim.org). We first tested models using all the 19 bioclimatic variables (Table A1), then ranked the most significant variables for each species based on jack-knife statistical tests of importance of different variables (Costion et al., 2015; Qin et al., 2017). To meet with multicollinearity assumption, highly correlated variables ($r > 0.9$ Pearson correlation coefficient) were excluded (Merow et al., 2013; Fourcade et al., 2014). The seven most significant and less correlated bioclimatic variables were then used in further modeling the distribution of suitable habitat for each species (Table 1). In our modelling, we employed 25% data for model testing and 75% for model training and set other values as default (Qin et al., 2017). The area under the receiver-operator curve (AUC) was used to evaluate the model performance in predictive accuracy and in estimation of species' suitable habitat range (Phillips et al., 2006, Merow et al., 2013; Costion et al., 2015; Qin et al., 2017). For species-specific modeling, we used 4 to 7 bioclimatic variables in our final set of modeling (Table 1). Habitat suitability values produced from MaxEnt analysis ranged from 0 to 1, and we defined the values into only two classes, representing 'unsuitable' (0–0.89) and 'suitable' (0.9–1) habitats. Thus, in calculating the projected range sizes, we only took into account and calculated the suitable habitats range size of species with high possibility ranges (between 0.9 and 1) (Costion et al., 2015). Further calculation of suitable habitat and production of maps were performed by ArcGIS ver. 10.1 (Esri, Redlands, CA). Statistical analyses were done in R (version 3.5.1) using *Vignettes* and *stats* packages.

2.6. Assessing origin and dispersal capacity

We conducted an exhaustive search of peer-reviewed literature for information on the dispersal syndrome of each tree species (Appendix B). Where data were unavailable for the targeted species, we used data for closely related congeneric species. We also sought information on the evolutionary time and geographic area of origin of the study species (often to higher-level lineages).

3. Results

3.1. Climate trends

In the study region, the annual mean temperature showed a warming trend over the past 116 years (1901–2017) ($r^2 = 0.232$, $p < 0.001$), with an average increase of 0.068 °C each ten years (Fig. 2a). In addition, the yearly maximum temperature ($r^2 = 0.179$, $p < 0.001$) and yearly minimum temperature ($r^2 = 0.191$, $p < 0.001$) also increased during the past century (Fig. 2a). A trend of decreasing precipitation was also detected ($r^2 = 0.126$, $p < 0.001$) (Fig. 2b).

3.2. Species' range dynamics and their evolutionary lineages

Altogether 20 tree species, belonging to 16 genera and 11 families, provided data useful for inferring range dynamics along altitudinal gradients (Table 2). Based on our assumption, We qualitatively categorized species as 'upward extension' being 12 tree species, i.e., *Adinandra megaphylla, Betula alnoides, Castanopsis tribuloides, Cinnamomum tamala, Eriobotrya bengalensis, Lithocarpus magnificus, Lithocarpus wallichianus, Rhododendron arboreum, Schefflera delavayi, Symplocos dryophila, Symplocos lucida* and *Viburnum cylindricum* (Fig. 3). Upward extending species have higher proportion of juvenile to adult trees individuals at upper altitudinal bands (except *Betula alnoides*) (Fig. 3; Fig. 5a). For most of the species, the mean DBH at upper altitudinal bands were generally smaller than those at lower altitudinal bands (Fig. 3).

We also categorized the eight species as 'non-upward', i.e., *Lithocarpus xylocarpus, Litsea monopetala, Lyonia ovalifolia, Myrsine semiserrata, Osmanthus yunnanensis, Quercus semecarpifolia, Pinus kesiya* and *Viburnum erubescens* (Fig. 4). The non-upward category species possess low proportion of juvenile to adult trees individuals at upper altitudinal bands (except *Lyonia ovalifolia*) or have larger adult tree individuals with few juveniles which indicate poor recruitment trend at their upper limits (Fig. 4; Fig. 5b).

Among the 12 upward species, nine species belong to lineages that originated from tropical regions and three species belong to lineages from subtropics and temperate; these lineages all originated between the Paleocene and the Miocene (Table 3). All the non-upward species, with the exception of one species originated from tropical regions (e.g., *Lithocarpus*), originated from lineages that evolved in subtropical and temperate regions between the Cretaceous and Eocene. There were no marked differences in dispersal syndrome among species of the two range dynamics categories, which generally shared the same vectors (Table 2).

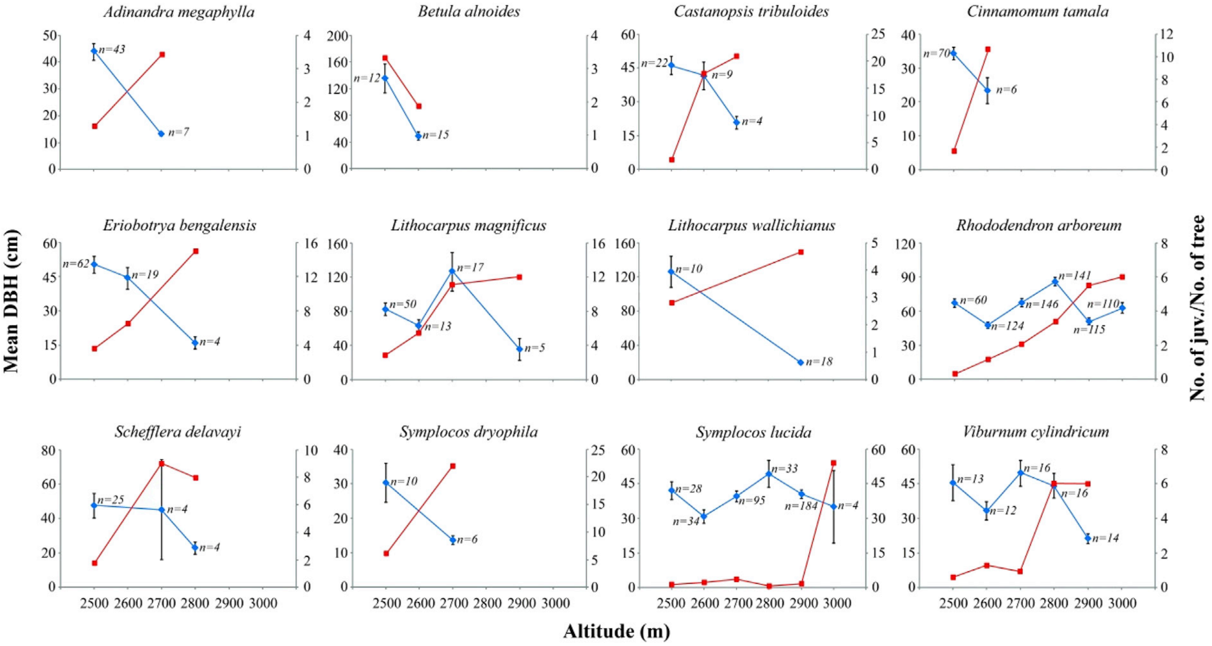

Fig. 3. Mean DBH and proportion of juveniles to trees representing upward category of species along altitudinal gradients, in Natma Taung National Park, Myanmar. Blue color = mean DBH, red color = proportion of juvenile to tree. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

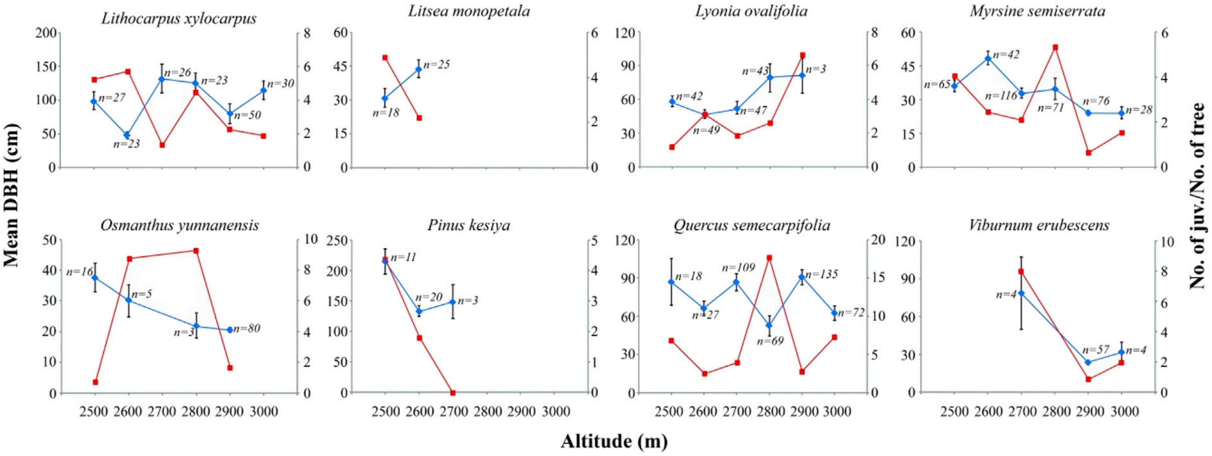

Fig. 4. Mean DBH and proportion of juveniles to trees representing non-upward category of species along altitudinal gradients, in Natma Taung National Park, Myanmar. Blue color = mean DBH, red color = proportion of juvenile to tree. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

3.3. *Range sizes estimated by habitat suitability models*

Habitat suitability models showed high AUC scores for all 20 species, attaining between 0.95 and 1. Estimated range size was marginally significant smaller for the upward species (mean = 452374 ± 85954 km^2) than for non-upward species (mean = 682007 ± 87419 km^2) (U test, $n = 20$, $U = 74$, $p = 0.047$) (Table 2) (Fig. A1, A.2).

4. Discussion

Our results suggest that most tree species in the study site extended their ranges upward while some others did not: response to climate change was species-specific. In general, our research supported a key prediction of the Climatic Variability

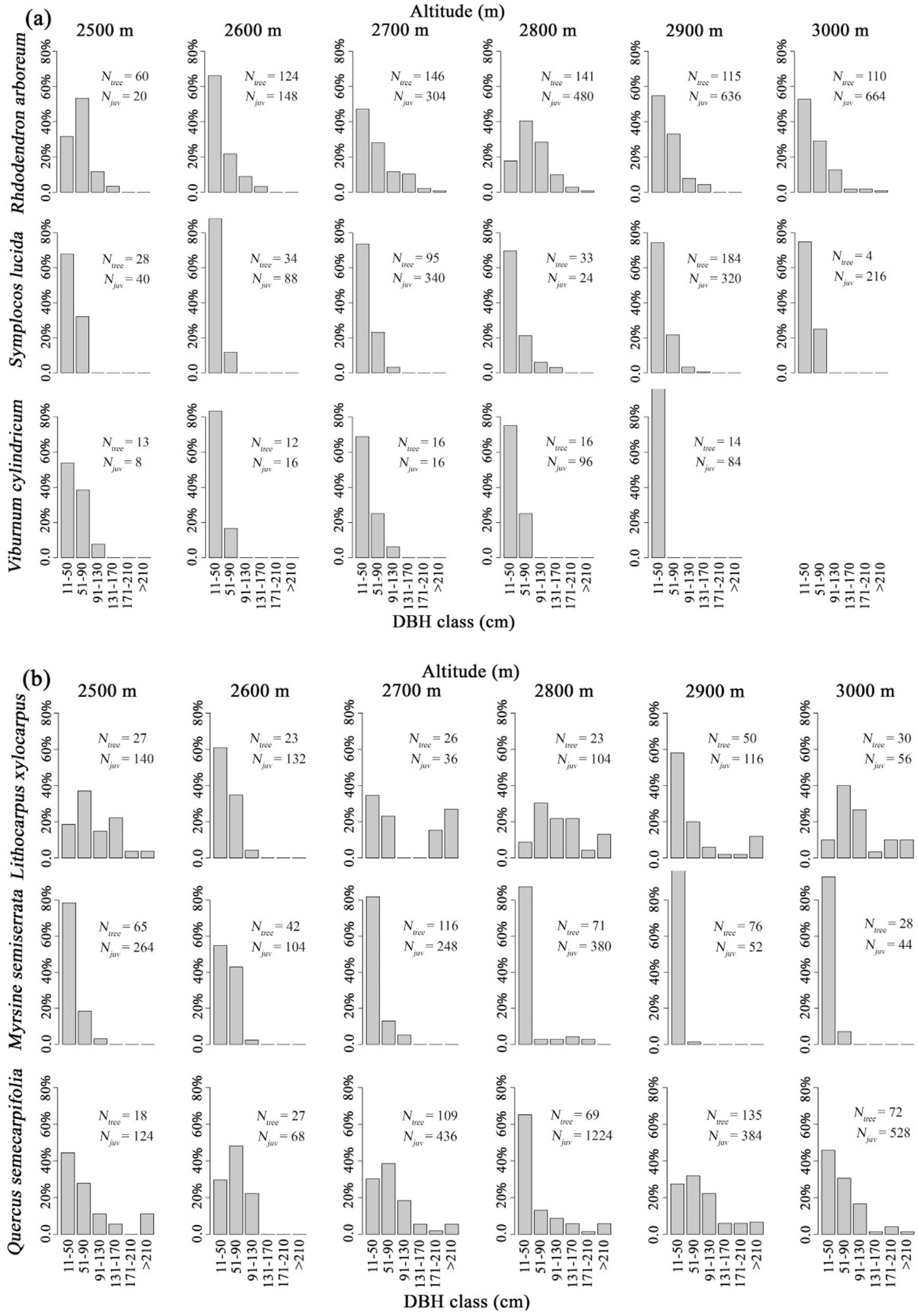

Fig. 5. Diameter classes and its proportion among all adult trees of (a) upward extending and (b) non-upward category species along altitudinal transect. The total number of adult tree (N_{tree}) and juveniles (N_{juv}) was indicated in each block.

Table 3
Origin and evolutionary history of species (at genus level) in different range dynamics categories.

Genus and range dynamics category	Origin and evolutionary history	Key citation
Upward		
Adinandra	**Tropics**, subtropics, *c.* 47 Ma, Middle Eocene	Yu et al. (2017); Rose et al. (2018)
Betula	Temperate**,** *c.* 25 Ma, Late Oligocene	Xiang et al. (2014); Bina et al. (2016)
Castanopsis	**Tropics,** *c.* 38–42 Ma, Middle Eocene	Cannon and Manos (2003)
Cinnamomum	**Tropics**, *c.* 55 Ma, Eocene	Huang et al. (2016)
Eriobotrya	**Tropics,** *c.* 15 Ma, Miocene	Li et al. (2011); Zhang et al., 2017
Lithocarpus	**Tropics,** *c.* 40 Ma, Eocene	Cannon and Manos (2003), Yang et al. (2018)
Rhododendron	Temperate, *c.* 65 Ma, Paleocene	Shrestha et al. (2018)
Schefflera	**Tropics,** *c.* 57 Ma, Eocene-Paleocene	Li and Wen (2014)
Symplocos	**Tropics,** *c.* 28–33 Ma, Oligocene	Manchester and Fritsch (2014)
Viburnum	Subtropics, *c.* 25–40 Ma, Oligocene-Eocene	Clement and Donoghue (2011)
Non-upward		
Lithocarpus	Tropics, *c.* 40 Ma, Eocene	Cannon and Manos (2003), Yang et al. (2018)
Litsea	Subtropics, *c.* 55–65 Ma, Early Eocene-Paleocene	Huang et al., 2018
Lyonia	Subtropics, *c.* 48 Ma, Eocene	Rose et al. (2018)
Myrsine	Subtropics, *c.* 50 Ma, Eocene	Rose et al. (2018)
Osmanthus	Temperate, *c.* 5–15 Ma, Late-Middle Miocene	Ha et al. (2018)
Pinus	Temperate, *c.* 133–140 Ma, Cretaceous	Falcon-Lang et al. (2016)
Quercus	Temperate, subtropics, *c.* 65 Ma, Paleocene	Deng et al. (2018)
Viburnum	Subtropics, *c.* 25–40 Ma, Oligocene-Eocene	Clement and Donoghue (2011)

Hypothesis (CVH), as the species that extended their ranges upward had relatively narrow distribution ranges compared to those that were non-upward. Furthermore, most of the upward-extending species were of tropical origin, while the non-upward species belonged to lineages with a deep evolutionary history in subtropical or temperate regions. The findings of this study also hold significant implications for the development of conservation strategies for tree species in mountainous regions of tropical Asia.

Species that responded to climate by shifting upslope had smaller geographic range sizes than those of the non-upward category. Species that experience high environmental variability generally have large range sizes (Dynesius and Jansson, 2000; Pintor et al., 2015). This suggests that species with wide climatic niches and large range sizes may be less impacted by climatic change than those with narrower niches and smaller range sizes. In this study, higher ratio of juveniles to trees occurred at most of the upward species at their uppermost altitudinal bands (Fig. 3; Fig. 5a), may imply that their seedlings seek for cooler habitats by running upslope under elevated climate warming. In contrast for the non-upward species, higher ratio of juveniles to trees mostly located at their mid-altitudes ranges or few juveniles are establishing at the upper limit where mature trees already existed (Fig. 4; Fig. 5b). This indicated that species with different environmental amplitudes and species-specific tolerances respond to climate gradients differently (Gaston, 2009; Pintor et al., 2015).

The species-specific response to climate change also means that different species may suffer distinct local extinction risk. In this study, the upward species distributed at low elevations, e.g., *A. megaphylla* and *C. tamala*, currently appear to be not in danger of extinction as they still have space to shift upward (Fig. 3). However, the upward species found at or near the summits, such as *R. arboreum* in this study, may face risk of mountain-top extinction, as the land area decrease with increasing elevations and they have nowhere to escape unless they acclimatize in their habitats. This implies that taxa distributing in tropical mountain area with narrow range sizes and narrow tolerances may face extinction with accelerated warming (Stevens, 1992; Morueta-Holme et al., 2013). For some upward species such as *L. magnificus* and *L. wallichianus*, range shift trends are sporadic, displaying an apparent leap-frog pattern, with gaps in some 100 m altitudinal intervals instead of continuous distributions (Fig. 3). Nevertheless, the upward species which already establishing near the summit are in danger of local mountain-top extinction as there is only several meters left to run upslope and escape. Certainly, some of them may have substantial lag time for long-lived tree species (Vetaas, 2002).

Some species showed no significant range shifts which may be due to other reasons rather than their high tolerant to climate change. For example, despite the presence of many large trees (>200 cm DBH) at the uppermost altitudinal band of *L. xylocarpus* and *Q. semecarpifolia*, very few juveniles of these species occurred at high altitude meadow grassland. The absence of upslope recruitment in these species may be limited not by abiotic conditions alone but by biotic interactions such as the ‘grass ceiling effect’ describing the inability of tree species to encroach into montane grassland (Rehm and Feeley, 2015). Such non-climatic barriers to upward range extension may increase the risk of local population extinction together with accelerated warming. In addition, we also found upward range extension of not only tropics origin species but also some temperate origin species under climate warming in this region. This finding supports the facts that some temperate lineages have diversified and due to heterogeneous environmental conditions their contemporary species diversity coincided in the tropics (Manchester and Fritsch, 2014; Shrestha et al., 2018; Tan et al., 2018). Thus, those species may track the climate warming and extend the ranges to cooler habitats at higher altitudes. However, for long-lived tree species, there may be a substantial lag time before extinction (Vetaas, 2002; Yang et al., 2018).

All the genera of the upward species originated in tropical regions (Table 2), except for three genera (*Betula*, *Rhododendron* and *Viburnum*) that originated from subtropical and temperate regions. However, two study species (*Betula alnoides* and

Viburnum cylindricum) from the genera *Betula* and *Viburnum* derived from clades that originated in tropics and warm subtropical Southeast Asia and southern China (Clement and Donoghue, 2011; Deng et al., 2018; Tan et al., 2018). Cooling and warming events in both Eocene-Oligocene and Quaternary period led diversification of many of the upward category species, in the tropics, with peak diversification in Oligocene-Miocene (Cannon and Manos, 2003; Li et al., 2011; Bina et al., 2016; Huang et al., 2016, Huang et al., 2018; Yu et al., 2017; Shrestha et al., 2018; Yang et al., 2018). In contrast, most non-upward species belong to widely distributed lineages with a deep evolutionary history in temperate regions of the Northern Hemisphere. After experiencing the Late Paleocene Thermal Maximum and early Eocene Climate Optimum, which interplayed in complex ways with tectonic movements, they became widely distributed over Europe, North America and high latitudes of Asia (Cannon and Manos, 2003; Wu et al., 2006; Deng et al., 2018; Ha et al., 2018; Huang et al., 2018; Rose et al., 2018). This suggests that these lineages were not severely affected by climate fluctuations, and not readily diversified during their long evolutionary histories, even during the Oligocene and Miocene Glaciations events, and persisted in their habitats. However, it should not be concluded that climate has no effect on these non-upward species. In fact, range sizes of the non-upward species are larger compared to those of the upward extending species. Thus, they seem more tolerate to climate fluctuations as they have wide environmental amplitudes and long life histories which help them to resist and exhibit less responsiveness to climatic change (Dynesius and Jansson, 2000; Cannon and Manos, 2003; Deng et al., 2018; Yang et al., 2018). Our results, therefore, revealed upward range extension of many tree species in a tropical montane forest. Under the scenario of climate change, as it is projected the continuing of temperature rises, the fate of tree species in tropical mountains are vulnerable particularly for tropics origin species.

In conclusion, our data on tree distributions suggest that many species have responded to climate warming by upward range extension, whereas others have shown no range shifts. Species from lineages of tropical origin were more likely to show upward shifts than species of subtropical or temperate origins. Generally, supporting the CVH, range dynamics of species belonging to lineages with a deep evolutionary history in high-latitude regions (which also had larger range sizes) were shown to be less responsive to climatic change than those of species from tropical lineages, which also had smaller geographic range sizes. Incorporation of biotic interaction and monitoring of juveniles in long-term, particularly at high elevations, could further contribute to understanding of species responses under changing climatic conditions. Further investigations on dispersal capacity and viability of each species and their interaction may advance the understanding of vegetation distribution and dynamics. Climate change is projected to accelerate and, rainfall and temperature are projected to become more variable. These changes may have stronger negative impacts on tropical montane communities, particularly for those species which have narrower tolerance ranges than those of high-latitude mountainous regions. Therefore, the landscape connection for those tropical montane species should be much critical for keeping their dispersal capacity and sustaining the recruitment, thus special attention need to be paid for effective conservation.

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Declaration of competing interest

None of the authors have any conflict of interest to declare.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e00973.

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