Drivers of elevational richness peaks, evaluated for trees in the east Himalaya

Suresh K. Rana iD,[1] Kevin Gross,[2] and Trevor D. Price iD[3,4]

[1]*Wildlife Institute of India, Dehradun 248001 India*
[2]*Biomathematics Program, North Carolina State University, Raleigh, North Carolina 27695 USA*
[3]*Department of Ecology and Evolution, University of Chicago, Chicago, Illinois 60637 USA*

Abstract. Along elevational gradients, species richness often peaks at intermediate elevations and not the base. Here we refine and test eight hypotheses to evaluate causes of a richness peak in trees of the eastern Himalaya. In the field, we enumerated trees in 50 plots of size 0.1 ha each at eight zones along an elevational gradient and compared richness patterns with interpolation of elevational ranges of species from a thorough review of literature, including floras from the plains of India. The maximum number of species peaks at similar elevations in the two data sets (at 500 m in the field sampling and between 500 m and 1,000 m in range interpolation); concordance between the methods implies that statistical artefacts are unlikely to explain the peak in the data. We reject most hypotheses (e.g., area, speciation rate, mixing of distinct floras). We find support for a model in which climate (actual evapotranspiration [AET] or its correlates) sets both the number of species and each species optimum, coupled with a geometric constraint. We consider that AET declines with elevation, but an abrupt change in the association of AET with geographical distance into the plains means that the location of highest AET, at the base of the mountain, receives range overlaps from fewer species than the location just above the base. We formalize this explanation with a mathematical model to show how this can generate the observed low-elevation richness peak.

Key words: beta diversity; diversification rate; elevational gradient; geometric constraints; Himalaya; mid-elevational peak; species richness; trees.

Introduction

As one proceeds from low elevations to mountain peaks, species richness in many clades does not show a monotonic decline (Grytnes and McCain 2013, Guo et al. 2013, Colwell et al. 2016). Instead, a richness peak at intermediate elevations seems to be the most common pattern (Rahbek 1995, 2005, Kessler et al. 2011, Grytnes and McCain 2013, Guo et al. 2013). A number of explanations have been proposed for this. They include climate (e.g., wetter conditions promote higher productivity at mid elevations; McCain 2009), source–sink dynamics on a bounded domain (Grytnes 2003), area of a particular elevational zone (McCain and Grytnes 2010), extinction of species or populations situated near the boundaries (Colwell and Hurtt 1994, Grytnes 2003, Colwell and Rangel 2010), and higher speciation rates at mid elevations (reviewed by Lomolino 2001, Grytnes and McCain 2013, Colwell et al. 2016). McCain (2009) considered tests for several of these hypotheses with respect to birds, finding support for a model in which climate, notably a

combination of water and temperature, was a strong determinant of richness patterns. However, in a general survey, Colwell et al. (2016) argue that boundary constraints contribute to the position of richness peaks and better match the data.

McCain (2009) and Colwell et al. (2016) reviewed multiple studies to assess the importance of climate and boundaries in setting the position of richness peaks. In this paper, we expand upon the hypotheses and tests proposed by McCain (2009), and evaluate each more rigorously than is possible from a survey of general patterns, by considering a single elevational gradient in depth. We study elevational correlates of tree species richness in the eastern Himalaya. Although no general review has specifically focused on trees, Guo et al. (2013) concluded that across the globe, tree richness generally peaked at mid elevations (on average 1,400 m), but some of the studies they included are subject to statistical biases, as we will describe. Studies in Nepal, Sikkim, and Bhutan have previously described elevational patterns for various plant groups, including all seed plants (Grytnes and Vetaas 2002, Feng et al. 2016, Kluge et al. 2017, Manish et al. 2017), trees specifically (Carpenter 2005, Bhattarai and Vetaas 2006, Behera and Kushwaha 2007, Acharya et al. 2011), and ferns and bryophytes (Bhattarai et al. 2004, Grau et al. 2007; see Appendix S1: Table S1). All

studies show a mid-elevation peak in species richness, but the position of the peak varies with sampling method and taxon (Appendix S1: Table S1).

We first show that tree richness peaks at a relatively low elevation, 500 m to 1,000 m, in the eastern Himalaya and then expand on the framework of McCain (2009) by considering eight prominent hypotheses. These include sampling artefacts, area, speciation rate, climatic effects, and dispersal on a bounded domain. We outline each hypothesis, concentrating on differences in our approach from earlier studies, and eliminating some a priori. Finally, we develop a simple mathematical model whereby a change in the slope of the relationship between climatic determinants of richness and geographical distance results in a richness peak at intermediate elevations.

Methods

We define a tree as a woody perennial plant, typically having a single stem growing to a considerable height and bearing lateral branches at some distance from the ground. Trees are the most prominent component of vegetation communities, are most easily surveyed, and are likely to have better information on elevational ranges in the secondary literature than other plant groups. We assessed richness patterns from both a literature survey and fieldwork.

Literature survey

We compiled elevational ranges from floras that list tree species from north Bengal and Sikkim (see map in Appendix S1: Fig. S1; Dash and Singh 2011, Ghosh and Mallick 2014), henceforth "local floras." A total of 850 species are present in these floras (Metadata S1). The floras document abnormally few species at low elevations, because of small land areas within political boundaries and limited sampling at these elevations, an issue that has been repeatedly noted in the literature (Grytnes and Vetaas 2002, Feng et al. 2016, Kluge et al. 2017). To correct for this, we examined two floras that cover the plains of West Bengal and Bihar (Hines 1978, Prain 1981), which resulted in extensions of lower elevational ranges of 213 species (25% of all species; 66% of these had lower limits previously recorded at 300 m or higher and 33% recorded down to 200 m; see Appendix S1: Fig. S2). If a Himalayan species is present in the plains, we set its lower elevational limit to be 100 m.

Fifty-three species (6.2%) are cultivated and the elevational ranges of 12 species (1.4%) were not reported, so we excluded these from analysis. Thus, we included 92.4% of the species that are found in the Himalayan region of Bengal and Sikkim according to the floras. We calculated the total number of tree species at each elevation from the documented lower and upper elevational range limits, assuming the range interpolation method, i.e., that the species occurs at all elevations in between.

Field sampling

S. K. Rana sampled discrete elevations at sites that were as little disturbed as possible across north Bengal and Sikkim. We sampled trees from eight elevational zones, which apart from the lowest and next highest zone, were separated by 500 m (Appendix S1: Fig. S1, Table S2). We worked within three protected areas, i.e., Chapramari Wildlife Sanctuary and Neora Valley National Park in north Bengal, and Khangchendzonga National Park in Sikkim. Because of the steep Himalayan terrain, it is generally not possible to study a single large plot, so we decided to enumerate trees on 50 small plots at each elevation of size 0.1 ha (31.65 × 31.65 m), for a total of 5 ha. Other studies have sampled small plots more dispersed across elevations, but this has made it difficult to assess local diversity at a given elevation (e.g., Ibanez et al. 2016). The first plot was selected as near to the indicated elevation as possible. In order to maximize counts of tree species at each elevation, we then traversed horizontally and set the next plot upon encountering a previously unrecorded tree species, or after 100 m, whichever came first. The elevational location of all plots was restricted to a band within 100 m of each designated elevation, with most clustering close to the designated elevation. However, the lowest elevation was in the plains (described in Rana et al. 2017), so that sampling was over a narrower elevational range than other locations. The elevation at 4,000 m had few tree species and here we simply recorded all species present. We recorded GPS information (latitude, longitude, and elevation) of every plot and girth at breast height (gbh) of every tree >30 cm in girth.

Because peaks in plant richness have generally been reported at mid elevations, we conducted additional surveys at two locations, at 200 m (27.06247° N, 88.77188° E; Rana et al. 2017) and at 2,000 m (27.0599° N, 88.7693° E). At both of these locations, we found a sufficiently flat location that we could survey a contiguous 5-ha area (200 × 250 m). In these plots all trees >30 cm in girth size have now been numbered with tree-tags. Every tree has been identified, and girth at breast height measured.

Trees were identified on site using floras (Polunin and Stainton 1984, Ghosh and Mallick 2014) and our own expert knowledge. In order to confirm identification, we photographed all species, preferably during the flowering or fruiting stage. If the identity of a tree was uncertain, a pressed specimen was taken to the Wildlife Institute of India, Dehradun herbarium. At present, 10 species included in the data set remain unidentified but eight of these are represented by single individuals. The complete data set is available as a supplement (Metadata S2).

Hypotheses and Tests

Sampling

Differences in sampling effort may lead to higher richness estimates at some locations than others (Lomolino

2001, McCain 2009), but even when sampling effort is constant, richness peaks may appear as artefacts. First, if upper and lower records are used to delineate a species elevational distribution, under-sampling results in an underestimation of the range, with a consequent estimate of high species richness at mid-elevations (Grytnes and Vetaas 2002). We have already noted this problem, because including records from the plains of India extends lower elevational limits and reduces the magnitude of the richness peak (Appendix S1: Fig. S2). This surely contributes to the inferred positions of many of the richness peaks assessed using interpolation methods, resulting in errors in summary reviews. For example, samples are usually taken only over a restricted portion of the entire elevational gradient, and even then a richness peak may be found between the highest and lowest elevation sampled (e.g., Oommen and Shanker 2005).

Field sampling (e.g., in a 5-ha plot) circumvents the interpolation problem but results in the recording of only a small fraction of the total richness, and raises issues of how to ascertain true richness at a location, especially if species abundance distributions differ (Gotelli and Colwell 2001, Lomolino 2001, Slik et al. 2015). For example, along a New Caledonian elevational gradient, Ibanez et al. (2016) showed that equal area plots with large trees tend to contain fewer individuals and hence fewer species than plots with small trees, which can obscure elevational trends. We used species accumulation curves and rarefaction in order to evaluate the extent to which species richness has been underestimated at each location (Gotelli and Colwell 2001). Given the different statistical issues associated with each method and the difference in scale, concordance between interpolation from the literature and local field surveys is taken to indicate the presence of a genuine peak in richness.

Competition between groups

A relatively neglected hypothesis for the presence of peaks at mid-elevations is that some groups may be competitively dominant at lower, more productive, elevations, and subordinates peak as these groups decline with elevation (Heaney 2001). This may well contribute to richness peaks of plant lifeforms other than trees along the east Himalayan gradient, such as shrubs, which reach a maximum at the point where tree richness is declining (Appendix S1: Fig. S3), and herbs above treeline, which show a peak at the point where shrub richness starts to decline (Bhatta et al. 2018). However, the relationship of shrubs to trees depicted in Appendix S1: Fig. S3, as well as more general considerations, suggest that trees are competitive dominants in the environments in which they occur, so we do not consider this hypothesis further.

Mixing of biotas

If two biotas from different biogeographic realms come together, the domain over which they co-occur may elevate richness. Mixing of temperate and tropical floras has been explicitly suggested as a cause of a richness peak in woody plants of the western Himalaya by Oommen and Shanker (2005). We tested this idea in two ways. First, we classified each species as having tropical or temperate affinities based on the affinities of the genus it belongs to, as compiled by Wu (1991). Second, we calculated species turnover between elevations (beta diversity) based on the presence/absence of species using the formula: $\beta = (b + c)/(2 \times a + b + c)$ where a is the number of species common to two elevations, b is the number of species unique to the first elevation, and c is the number of species unique to the second elevation. We predict that locations of high turnover represent a coming together of floras, and hence should also be the position elevated in species richness. Beta diversity includes a component due to species turnover and one due to richness differences, which may lead to circularity. We extracted the turnover component (βsim) following the recommendations of Baselga and Leprieur (2015) using the betapart package (Baselga and Orme 2012) in R (R Development Core Team 2018).

Area

Larger areas contain more species than smaller ones. If some climatic zones are larger than others, then they may contain more species (McCain 2009), driven largely by lower population extirpation and higher recolonization rates in these zones. We asked if area of elevational zone correlates with species richness.

The effect of area assumes that the size of the available pool is similar in different climatic zones as well as niche conservatism, so that the balance between extinction and recolonization at any given scale primarily depends on access from other climatically similar locations, rather than from above or below. We tested for niche conservatism by developing a phylogeny of all tree species in the east Himalaya following the method and global phylogeny of Qian and Jin (2016). The method assigns all unsequenced congenerics to a soft polytomy. Hence, this tree contains many, typically shallow, polytomies, which we broke in two ways to make a fully resolved phylogeny. First, we resolved the soft polytomies to a series of dichotomies with zero branch length between them using the APE function multi2di (Paradis et al. 2004). Second, we used the polytomy resolver program of Kuhn et al. (2011), setting a birth:death prior in BEAST 1.5.4 (Drummond and Rambaut 2007). We ran the program for 11.1 million generations, with output trees sampled from the posterior distribution every 1,000 generations. We extracted the last 100 trees; the last of these is shown in Appendix S1: Fig. S4. We calculated Blomberg's K metric (Blomberg et al. 2003) on these 100 trees (using the R package picante [Kembel et al. 2010] and calculated the mean $\pm$ SD). Values of $K > 1$ indicate niche conservatism, whereas those close to 0 indicate evolutionary lability. K correlates well with

other statistics on niche conservatism (e.g., Price et al. 2014). Results from the two methods of resolving soft polytomies were similar, and we present only those based on the birth : death model.

Diversification

Diversification is similar to area in that it considers rates and/or time for species accumulation to be a property of a climatic zone, with transgressions between zones to be rare. While a popular hypothesis for richness patterns, in its simplest guise, it is not a hypothesis to be compared to the others. This is because in a phylogeny connecting all species in a location, the total number of species is the product of average diversification rate and time to the root, so average diversification rate should generally correlate with richness (Wiens 2011). However, one can ask if locations with more species also contain species that are members of recently radiating groups, which, given a strong assumption that speciation rates at present are similar to those in the past, suggests a contribution of speciation rate to species richness. For example, more topographical barriers in some elevational zones than others may have led to higher speciation rates and hence greater species accumulation. We addressed this question in three ways.

First, we plotted species : genus ratios along the elevational gradient, assuming that high ratios represent more actively radiating groups. Species : genus ratios should statistically correlate with species richness (Gotelli and Colwell 2001). We evaluated the species : genus ratio against a null model following Krug et al. (2008) whereby we permuted species and their elevational limits among genera 1,000 times, each time computing the species : genus ratio along the gradient. Second, we plotted the fraction of endemics (species confined to the Himalaya) assuming that any speciation effect on richness would be a result of within-Himalaya speciation. Third, we used the resolved phylogeny to estimate recent speciation rates; again results were similar independent of method of resolving the soft polytomies, and we only present those from the birth–death model. We computed species diversification rates (the DR statistic of Jetz et al. 2012), for each of the 100 trees from the posterior distribution and calculated the average. The DR statistic for a species asks how many nodes lie between the species and the root, weighting nodes closer to the present more strongly. Hence it is roughly an estimate of instantaneous present-day speciation rate for that lineage; simulations have shown it to be useful because it is relatively insensitive to species richness (Oliveira et al. 2016). We computed the average DR statistic for all species in a given elevational zone, which is equivalent to asking if species that belong to recently diversifying clades are concentrated in certain locations.

Climate

Climate variables generally correlate with tree species richness. Ricklefs and He (2016) analysed 47 tree plots across the world (with a median size of 25 ha) and found temperature of the warmest season and lack of seasonality to be strongly positively correlated with number of tree species. They noted that both these measures are correlated with actual evapotranspiration (AET; see Appendix S1: Fig. S9) and hence plant productivity (Storch et al. 2006), which has more generally been found to be an important correlate of plant species richness (Currie and Paquin 1987, Kreft and Jetz 2007). The correlation between climate and tree species richness remains agnostic to mechanism, which includes both present day productivity (e.g., more annual plant growth enables finer niche partitioning; Currie and Paquin 1987), and a relationship arising from past history (e.g., age and area promoting species accumulation, both of which are greater for tropical climates; Fine and Ree 2006, Fine 2015). Both present day and historical processes are likely to be important (Silvertown 2004, Kraft et al. 2008), and it may even be that temperature is more related to historical explanations, and water to contemporary ones (e.g., Latham and Ricklefs 1993). Here, we are simply concerned with the prediction that, if climate is a determinant of a richness peak, that peak should coincide with a maximum in actual evapotranspiration (McCain 2009).

Unfortunately, the way by which climate varies along the east Himalayan gradient remains uncertain, given the few on-ground climate stations available; an uncertainty that is often unrecognized but applies to many other regions in the tropics (Soria-Auza et al. 2010). According to worldclim.org (Hijmans et al. 2005) and the CHELSA data set (Karger et al. 2017), both precipitation and temperature show a decline from 100 m to the highest elevations, albeit with much scatter (Appendix S1: Fig. S5). Modeled AET shows a similar pattern (Fig. 1; Appendix S1: Fig. S5; Trabucco and Zomer 2010). On the other hand, remote sensing (Bookhagen and Burbank 2010) and models based on measured atmospheric pressure and topography (Gerlitz et al. 2015) suggest a peak in precipitation at 500 m. In
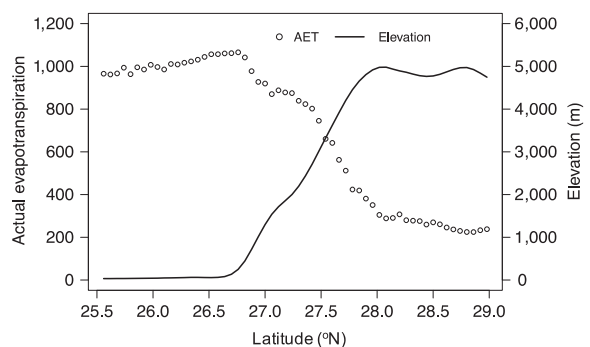

Fig. 1. Distribution of modeled actual evapotranspiration (from Trabucco and Zomer 2010) and elevation against latitude for 2,000 points drawn from Sikkim and the most northerly district of north Bengal. Points are averaged into 58 latitudinal bins.

these latter analyses, after outliers are excluded, the models explain a relatively low fraction of precipitation recorded at known climate stations across the entire Himalaya (Bookhagen and Burbank 2010, Gerlitz et al. 2015). Hence, we consider the inferred 500-m peak in these papers to remain uncertain.

Climate data are available for seven stations between 700 m and 4,200 m in Sikkim, which does not allow one to separate the alternatives, but confirms a strong linear decline of precipitation ($r = 0.99$) and temperature ($r = 0.99$) with elevation along this portion of the gradient (Acharya et al. 2011). The Indian Meteorological Department reports a value of ~3,450 mm at 100 m in Jalpaiguri (relatively close to our low-elevation site, coordinates: 55.501 N, 37.33 E, elevation 150 m), higher than that recorded at the lowest elevation in Sikkim by Acharya et al. (2011) (~3,350 mm at 700 m), and consistent with an increase in precipitation into the plains. In our analysis, we consider that the maximum AET occurs at the lowest elevation and declines with elevation as suggested by Fig. 1, while leaving open the possibility that the maximum may actually be slightly higher.

Geometric constraints: Extinction on a bounded domain

A set of theories for mid-elevation richness peaks are based on geometric constraints (Colwell and Hurtt 1994). In the simplest model a random shuffling of ranges on a bounded domain leads to a mid-elevation richness peak and zero species at the domain boundaries; the model is modified in various ways to make it more realistic (see Colwell et al. [2016] for a recent review). Grytnes (2003) considered the underlying mechanisms that might drive these constraints. Assuming the presence of hard boundaries at each end of the domain that species cannot cross, such as a coastline at low elevations, Grytnes (2003) suggested that populations or entire species that occupy the edge of the domain suffer greater extinction rates. First, if climate conditions fluctuate, then the conditions at the bottom and top may regularly disappear, whereas conditions in the middle are preserved, albeit while shifting position (Grytnes 2003, Colwell and Rangel 2010). Second, if species at range edges have smaller ranges then they are more likely to go extinct. In the current study, the lower elevational limit does not abut a hard boundary such as a coastline, but instead the species range can extend into the plains. A large area extends south from the Himalaya, which seems to make extinction at the lowest elevations less likely than at intermediate elevations. We do not consider this hypothesis further.

Geometric constraints: Range extensions on a bounded domain

An alternative mechanism driving geometric constraints is that of range expansion (Grytnes 2003). In the center of a bounded domain, locations can receive dispersers from both above and below, whereas at the edges locations can only receive from one direction. A feature of this model is that range sizes are smaller at the edges of the domain than in the center. We develop a variant of this in the model section below, whereby step changes in the relationship of climate to geographical distance generate a similar pattern, because dispersers from outside the domain are already represented inside the domain.

RESULTS

Data

We encountered a total of 269 tree species (34% of those in the literature). The maximum number of species was at 500 m (106 species, Fig. 2). The true number of species at every elevation was underestimated to an unknown degree. However, species rarefaction (Appendix S1: Fig. S6) implied that the 500 m elevation was the least well sampled when compared to other elevation zones: as the sample size increases from 40 to 50 plots, more new species continued to be encountered at this elevation than higher up, due to the presence of many rare species (Appendix S1: Figs. S7, S8, Table S3). This suggests that the 500 m zone indeed has the highest local species richness along the elevational gradient. At 200 m and at 2,000 m, we surveyed an additional single 5-ha plot as well as the multiple small plots described so far. The results are similar between the two methods (Appendix S1: Table S2), showing a much higher number of species in the foothills than at mid elevations (2,000 m). The total number of species increased by 23% (84 to 103) after addition of the second 5-ha sampling area at 200 m, whereas, at 2,000 m, the species number increased by only 6% (49 to 52). This is consistent with the rarefaction results and implied that lower elevations were relatively under-sampled.
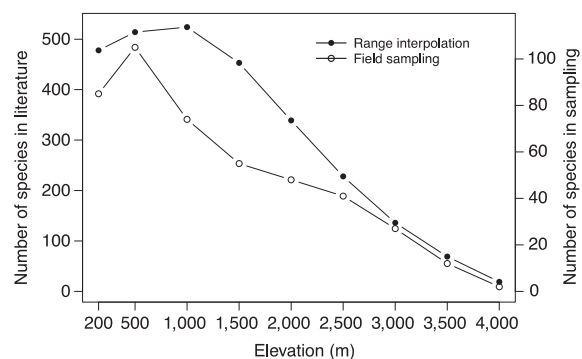

FIG. 2. Tree species richness along the elevational gradient in the eastern Himalaya based on the number of species encountered in 5-ha sampling areas at nine elevation zones and overlap of ranges inferred from upper and lower limits given in the secondary literature.

Interpolation of elevational ranges of 785 species from local floras, including the addition of plains records, shows that species richness is relatively high and approximately the same at 500 m and 1,000 m (Fig. 2). Given that the richness peak arises in a similar position in both the literature compilation and field samples, we conclude it is real.

Mixing of biotas

Both the literature survey and field samples indicated that the highest species turnover is between 1,500 m and 2,000 m (Fig. 3a, b). The number of species encountered was very similar at these two elevations in the field data (54 and 49 respectively, Appendix S1: Table S1), implying a large turnover in composition. This was confirmed by a partitioning of beta-diversity into the turnover component (solid circles in Fig. 3a, b). These results suggest that the 1,500 m to 2,000 m belt is an important transition zone between sub-tropical and temperate vegetation

in the east Himalaya. Hence the 500-m peak is too low to be simply accounted for by mixing, a conclusion that was supported by separating species into those with tropical and temperate affinities: the peak occurred within the tropical flora (Fig. 3c). Li and Feng (2015) and Kluge et al. (2017) demonstrate similar results from subsets of the data we present, based on the Nepal and Bhutan floras, respectively.

Area

Fig. 4a shows the distribution of area in different elevational belts. The richness peak (500–1,000 m) belt spans a relatively small area, as is also true across a larger segment of the eastern Himalaya (Price et al. 2014), as well as when Bhutan is considered alone (Kluge et al. 2017). Hence, area seems to play little role in driving the richness peak, as observed in other studies (McCain 2009, Karger et al. 2011).
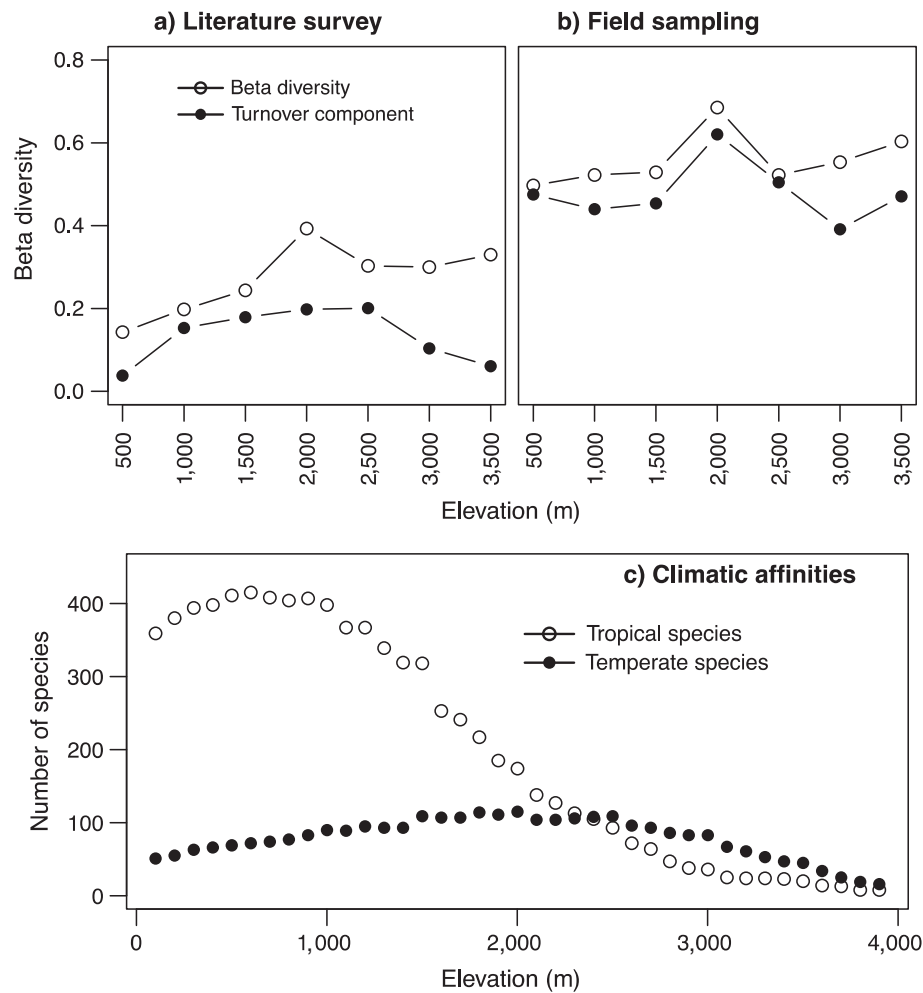

Fig. 3. Beta diversity and climatic affinities along the elevational gradient in eastern Himalaya determined by (a) presence of species at elevational zones based on interpolated ranges from the published literature, (b) presence of species during field sampling of trees at different elevations, and (c) elevational richness of species belonging to tropical and temperate genera.
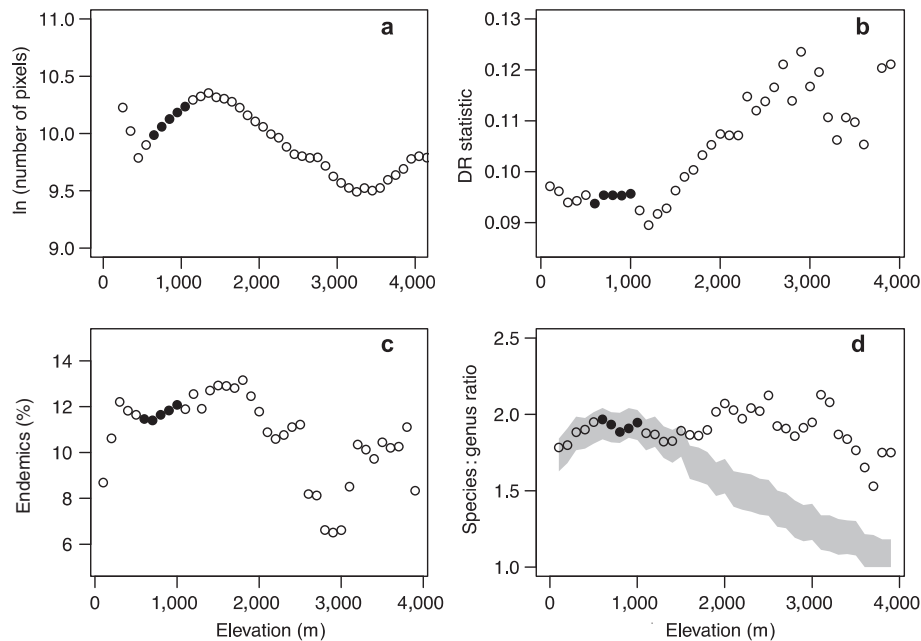
FIG. 4. (a) Log (base *e*) of number of pixels in the Digital Elevation Model of the study area. (b) Average diversification rate (DR) of species in every 100-m elevational band. (c) Elevational richness of endemic tree species. (d) Elevational pattern of species to genus ratio of trees (circles show species to genus ratios based on actual elevational ranges and the shaded area represents the 95% confidence interval from a null model based on 1,000 random shuffles of the species and their ranges across genera). Panels b–d are based on the literature survey (not the field data). In each panel the black points represent the elevation zones spanning the highest richness.

Speciation rate

Both the speciation rate and area hypotheses depend on niche conservatism. For range midpoint, we found the estimate of phylogenetic conservatism, $K = 0.04 \pm 0.017$ (mean $\pm$ SD; SD based on replicates across 100 trees output from the Bayesian analysis) and for range size $K = 0.01 \pm 0.003$. These values are exceptionally low, implying a great deal of lability: related species often occupy different elevational zones, which limits the applicability of the area and speciation rate hypotheses. In accordance with this, the species-genus ratios are higher than expected only above about 1,800 m, the fraction of endemics is largely invariant up to 2,000 m and the DR statistic is relatively low at the richness peak and highest at 3,000 m (Fig. 4b–d). These results all imply that species belonging to actively diversifying groups are not associated with the richness peak.

Climate

The decline of inferred AET with elevation (Fig. 1) correlates well with species richness patterns (using elevation and the points as in Fig. 2, $r = 0.93$, $N = 8$, for the field data, and $r = 0.95$, $N = 9$, for the literature survey). While explaining a large fraction of the variance, if climatic controls alone were responsible for the richness patterns, a monotonic decline in AET would not predict a richness peak. However, if AET actually peaks at

500 m, as atmospheric measurements and models suggest may be the case (Bookhagen and Burbank 2010, Gerlitz et al. 2015), then AET may perfectly correlate with richness patterns. In what follows, we assume that AET declines with elevation (Fig. 1, see also Appendix S1: Fig. S5 where we show a similar pattern of decline based on climatic data set taken from Karger et al. 2017), and investigate the consequences of boundaries at the lowest and highest elevations.

Model

We now introduce an explanation for intermediate richness peaks on a bounded domain, where domain limits are set by a step change in an environmental variable. Our model was based on the environmental geometry model of species richness gradients described in Gross and Snyder-Beattie (2016). We assumed that the edges of the domain constitute boundaries across which there is no geographical barrier preventing a species from extending its range, but across which the slope of the relationship between AET and geographical distance changes (e.g., Fig. 1). The main assumptions are that (1) AET positively correlates with the number of species whose optimal growth rate is at that location (Appendix S1: Fig. S9) and (2) identities are also set by AET so that few new species are added once we reach the plains. Then, if we consider three locations in order from bottom to top of the mountain, the location in the

middle contains optimal conditions for fewer species than the one at the bottom, but ranges from species whose optima lie both above and below the middle may overlap, potentially inflating richness above that of the bottom.

To formalize this model, we rescale the elevation gradient to lie between 0 and 1. Define a species optimal elevation to be x_o and its elevational tolerance to be γ. A species range spans elevations $x_o \pm \gamma$ unless either or both limits extend beyond the domain edge ($x_o - \gamma < 0$ and/or $x_o + \gamma > 1$). If the lower elevational limit of a species evaluates to less than 0, then we re-set the lower elevational limit to 0, and the range extends on to the lowland plain. A similar adjustment is necessary for species whose upper elevational limit extends on to the Himalayan plateau. Thus, the species' elevational range extends from a lower limit of $(x_o - \gamma) \vee 0$ to an upper limit of $(x_o - \gamma) \wedge 1$, where $\vee$ and $\wedge$ stand for maximum and minimum respectively. A consequence of this formulation is that species elevational ranges are smaller at domain edges (Appendix S1: Fig. S11c), which in our data is especially true for the lower limit (Appendix S1: Fig. S10).

First, consider a fixed value for γ. Of the species with an environmental tolerance equal to exactly γ, the proportion that occur at elevation x along the gradient is given by

$$S(x; \gamma) = \Pr\{(x - \gamma) \vee 0 \leq x_0 \leq (x + \gamma) \wedge 1 | \gamma\}. \quad (1)$$

The lower-elevation and upper-elevation boundaries for x_0 in Eq. 1 are exactly the same as the lower and upper elevational limits of a species whose elevational optimum occurs at x_0. Of all species, the proportion that are found at elevation x, $S(x)$, is obtained by integrating Eq. 1 over the marginal distribution of γ

$$S(x) = \int S(x; \gamma) \, dF(\gamma)$$
$$= \int \Pr\{(x - \gamma) \vee 0 \leq x_0 \leq (x + \gamma) \wedge 1 | \gamma\} \, dF(\gamma). \quad (2)$$

To illustrate this, Fig. 5 shows an example of a richness gradient under the following inputs. We assume that the distribution of species optimal environments, x_0, aligns with AET, but allow 10% of species to have their optimal locations beyond the gradient, i.e., on the plains and encroach on to the gradient (setting this value to 0 makes no qualitative difference, Appendix S1: Fig. S12), and 90% have optimal elevations that occur on the interior of the gradient. Second, of those species with optimal elevations on the interior of the gradient, their elevational optima are drawn from a beta distribution with a density that declines linearly from the base of the gradient to its top (Appendix S1: Fig. S11a). Species elevational tolerances (γ) are drawn from a separate, independent beta distribution with mean of 0.2 and standard

deviation of 0.1 (Appendix S1: Fig. S11b). This distribution reflects an assumption that species with narrow elevational niches are more common than species with broad elevational niches. While these inputs are loosely informed by our data, they are not formal estimates, but instead illustrate how a monotonic gradient in AET combined with a step change in the relationship of climate to distance can yield a low-elevation diversity peak. As the relationship of AET with richness increases, the position of the peak is expected to be lower down the mountain, and elevational range sizes become relatively smaller at lower elevations (Appendix S1: Fig. S12).

DISCUSSION

According to Trabucco and Zomer (2010) actual evapotranspiration (AET) declines with elevation in the east Himalaya (Fig. 1), and hence correlates with the general decline in tree species richness from low to high elevations. Any other elevational correlate may also explain the strong correlation of tree richness with climate, although what these might be is unclear. Previous studies along east Himalayan elevational gradients have specifically invoked climate, both precipitation and temperature (Acharya et al. 2011) and precipitation and temperature seasonality (Li and Feng 2015), as drivers of plant richness patterns, in accordance with both our inferences and global analyses of plants (Kreft and Jetz 2007) and trees in particular (Ricklefs and He 2016).

The question remains of how the strong correlate of climate with species richness arises. The correlation may have arisen for historical (e.g., age and area) reasons (Fine 2015). It may also reflect present day conditions. First, a greater number of individuals may lead to a greater number of species (Currie et al. 2004), but tree density does not vary greatly along the gradient (Appendix S1: Fig. S13) and is not correlated with species numbers (Appendix S1: Table S4, $r = -0.06$). Second, maximum tree height has been invoked as a measure of environmental "harshness," which is thought to more directly affect richness (Marks et al. 2016). We do not have data on height, but girth varies erratically along the gradient (Appendix S1: Fig. S13). Particularly large trees at 500 m (*Terminalia myriocarpa*, *Tetrameles nudiflora*) correspond to the peak in species numbers, so perhaps this is indeed the optimal climatic zone, but we are cautious in this interpretation because extremely large trees are found on the plains, even if they are not present in our study site. Further, some trees are larger at 2,000 m (e.g., *Quercus lamellosa*, *Machilus duthiei*) than any at 200 m and 1,000 m despite the number of species being about one-half of the number at lower elevations. It is possible that these patterns reflect some unknown disturbance in the past (e.g., by humans), but it may also be a consequence of the way species invest at these elevations, again raising the issue of how climate affects species richness, if it is indeed attributable to current conditions.
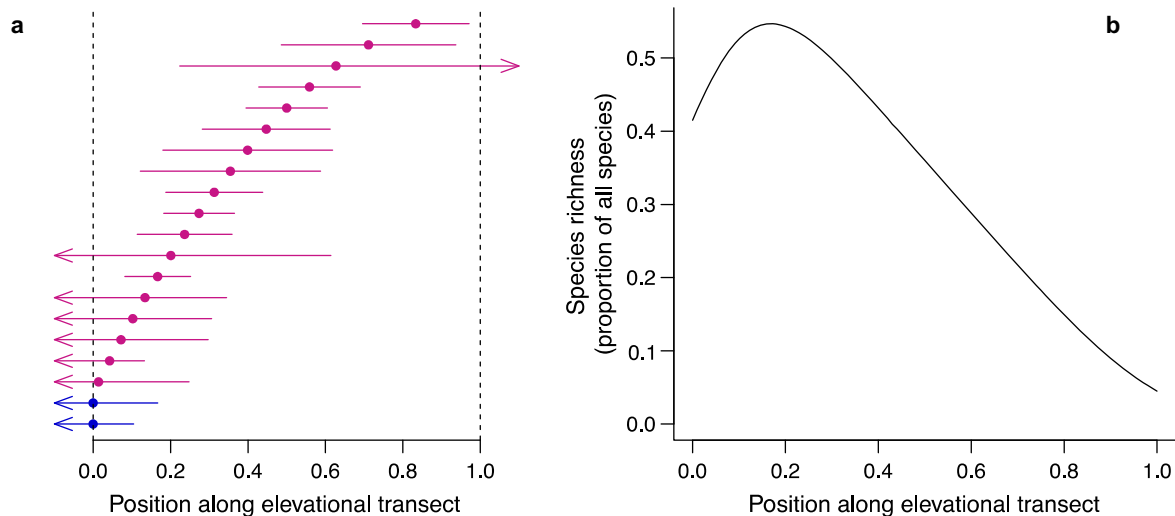
FIG. 5. (a) Each horizontal line shows a species elevational range in a single rendition of the model. The dot corresponds to the species' optimal elevation. Ranges shown in blue correspond to species whose optimal elevation occurs on the lowland plain bordering the $x = 0$ end of the gradient. Ranges shown in violet correspond to species whose optimal elevations occur in the interior of the gradient. Arrows denote ranges that extend on to the neighboring lowland plains, or the high Himalaya. (b) Example of species richness gradients, as calculated from Eq. 2. The vertical axis shows $S(x)$, the proportion of species ranges that include the elevation given by x. In this simulation, optimal elevations and elevational tolerances are assumed to be independent. Here 10% of species encroach on the gradient from the lowland plain and the remaining 90% of species have optimal elevations on the interior of the gradient. Of those whose optimal elevations lie on the gradient's interior, elevational optima are weighted toward the lower elevations, reflecting an underlying productivity (AET) gradient. These simulation settings are the same as those that generated the sample ranges shown in panel a.

Whatever the mechanism underlying the richness–climate association, the apparent monotonic decline of AET with elevation (Fig. 1) and strong association of AET with species richness (Appendix S1: Fig. S9) suggest that AET alone cannot explain the presence of a peak in richness at an intermediate elevation, which we have shown is at 500–1,000 m for trees. We consider three alternative climate-related explanations for the peak. First, Kluge et al. (2017) argued that a quadratic influence of temperature could explain a plant richness peak in Bhutan, with an intermediate temperature optimum, and richness declines both above and below this value. The suggestion has not been raised previously, and seems unlikely given the importance of water variables in other studies, and the generally large number of species found in tropical rainforests. Second, the peak is particularly pronounced at 500 m in the field samples, but the topography is heterogeneous at 500 m, much more so than at 200 m. Hence, we sampled over a relatively broader elevational range, and by implication a broader scope of climate, when compared with the 200 m elevation, which spans flat terrain in the plains (200 m, elevation 218 ± 12.6 m [mean $\pm$SD]; 500 m, 541 ± 31.9 m; $N = 50$ 0.1-ha plots in both locations). We discount this as a cause of elevated richness, not only because the peak at 500–1,000 m also appears in the literature survey, but because the average number of trees on single 0.1-ha plots was 20% higher at 500 m than 200 m (9.86 at 200 m, 11.84 at 500 m). Hence the difference between elevations arises at the "within-plot" level

and not the "between-plot" level, and cannot be attributed solely to sampling over a potentially wider range of climatic conditions. A third climate-based explanation is that precipitation, and hence AET, in fact peaks at 500 m rather than declining monotonically from the base (Bookhagen and Burbank 2010, Gerlitz et al. 2015). The test of this possibility requires additional on-ground climate stations, but some data sets infer that precipitation is higher on the plains. For the purposes of the rest of this discussion, we assume that AET monotonically declines with elevation and consider alternative explanations for the richness peak.

Several other hypotheses for richness peaks are not supported in the data. These include "present day" speciation rates. As estimated from the phylogeny, species belonging to clades with currently high diversification rates are more common at elevations beyond 1,500 m and not at the richness peak (Fig. 4b), a pattern also seen in birds (Price et al. 2014, Quintero and Jetz 2018). This implies that many of the species at lower elevations were formed in the relatively distant past. Further, evidence against the importance of not only diversification but also area comes from the exceptionally high phylogenetic lability in both range position and range size, with K values close to zero, implying that transitions between elevational bands have happened often. For example, of the two species of *Aesculus*, one's midpoint is at 1,050 m, below the freezing line and the other's is at 2,400 m, above the freezing line. Similarly, among 33 and 15 species in the genera *Ficus* and *Litsea*,

respectively, most of the species grow at low elevations, but a single species of each has its range midpoint lying above 2,000 m.

We suggest that a domain boundary contributes to the presence of a richness peak just above the lowest elevation. In this case, the boundary is that of a step change in the association of geographical distance with climatic conditions. In the original mid-domain models of boundary constraints, the predicted richness peak lies at the center of the domain, because when elevational ranges are shuffled on the domain, species with large elevational ranges commonly overlap at the midpoint (Colwell and Hurtt 1994). The way boundary constraints arise in the mid-domain models has been given biological interpretations. The two most commonly proposed are limits on range extensions across the boundary and local extinction at boundary edges (Colwell and Hurtt 1994, Grytnes 2003, Colwell and Rangel 2010). We extend these interpretations to that of a state change in the relationship between geography and climate. At the base of the Himalaya, few new species are found further to the south because climate to the south is similar to that at the base, hence range expansions from outside the domain contribute few new species to the domain. The position of the peak does not lie in the middle of the domain, because we assume that the optimum for a given species is determined by a certain AET value, and the number of species that can be maintained at a location correlates positively with AET. This means that many species have their optima near the base of the mountain, and elevational ranges that abut the lower domain boundary are truncated. The model reproduces a low elevation peak and predicts elevational ranges to be relatively smaller at lower elevations than in the middle (Appendix S1: Fig. S10), as is true in the data (Appendix S1: Fig. S7).

Several previous models have integrated geometric constraints with productivity as a cause of peaked richness patterns (e.g., Storch et al. 2006, reviewed in Colwell et al. 2016). Most recently, Colwell et al. (2016) built a model whereby, as in the original mid-domain models (Colwell and Hurtt 1994), empirical range sizes of species are fixed. They randomly place species midpoints on the domain according to a normal distribution truncated at the domain boundaries (termed the attractor distribution), subject to the geometric constraint, in the best fitting algorithm, that if a species midpoint is placed so that its range overlaps the domain edges, the midpoint is shifted to the interior just sufficiently to abut the domain edge (this is one way the model differs from ours, because we truncate ranges whenever the potential range overlaps the boundary.) The attractor distribution may result from a humped gradient in environmental favorability, such as AET (Colwell et al. 2016), or from some of the other alternatives we have described. In some of the examples Colwell et al. (2016) considered, the peak of the modeled attractor distribution is close to the domain edge, producing a richness pattern similar to that observed in our model.

A consequence of the model presented in this paper is that species abutting the lower domain limit have asymmetric elevational distributions about the optimum, with a greater range of elevation, and, by inference, environmental conditions, experienced above the optimum than below. One explanation may lie in source–sink dynamics, whereby all species have a similar range of environmental conditions over which they can maintain positive growth (birth greater than death), but dispersal creates sinks on both sides for species at mid elevations, and only on one side at the domain edges (Grytnes 2003). However, Colwell et al. (2016) noted that species abutting domain boundaries may genuinely under-fill their niche. For example, in the case we have considered where the boundary is not set by a coastline, species whose ranges extend into the plains may be more limited to the south by biotic factors such as competition, whereas abiotic factors influence evolution of the fundamental niche more strongly toward higher elevations. The freezing line is at about 1,800 m in the eastern Himalaya (data extracted from Worldclim; Hijmans et al. 2005) and the average range size for species at 200 m is 1,300 m (Appendix S1: Fig. S10).

Conclusions

In summary, in the eastern Himalaya we have evidence that a peak in tree species richness lies just above the lowest elevations. We argue that this is driven by relationships of climate with species richness and identity and the changing relationship of climate with geographical distance, as the base of the mountain meets the plains. What is now required is a comparison of the alternative models based on the distribution of elevational range sizes and positions, plus mechanistic investigations. For example, we need a better understanding of why species abundance distributions vary along the gradient, and in particular why at some elevations a few tree species are particularly dominant (Appendix S1: Figs. S7, S8). We suggest this will come from an incorporation of historical analyses, together with detailed studies of individual species.

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